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Multi-gene phylogeny and taxonomy of *Amauroderma* s.lat. (*Ganodermataceae*)

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Key words

Ganodermataceae
morphology
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ultrastructure

Abstract *Amauroderma* s.lat. has been defined mainly by the morphological features of non-truncate and double-walled basidiospores with a distinctly ornamented endospore wall. In this work, taxonomic and phylogenetic studies on species of *Amauroderma* s.lat. are carried out by morphological examination together with ultrastructural observations, and molecular phylogenetic analyses of multiple loci including the internal transcribed spacer regions (ITS), the large subunit of nuclear ribosomal RNA gene (nLSU), the largest subunit of RNA polymerase II (*RPB1*) and the second largest subunit of RNA polymerase II (*RPB2*), the translation elongation factor 1-α gene (*TEF*) and the β-tubulin gene (*TUB*). The results demonstrate that species of *Ganodermataceae* formed ten clades. Species previously placed in *Amauroderma* s.lat. are divided into four clades: *Amauroderma* s.str., *Foraminispora*, *Furtadoa* and a new genus *Sanguinoderma*. The classification of *Amauroderma* s.lat. is thus revised, six new species are described and illustrated, and eight new combinations are proposed. SEM micrographs of basidiospores of *Foraminispora* and *Sanguinoderma* are provided, and the importance of SEM in delimitation of taxa in this study is briefly discussed. Keys to species of *Amauroderma* s.str., *Foraminispora*, *Furtadoa*, and *Sanguinoderma* are also provided.

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INTRODUCTION

Amauroderma was established by Murrill (1905) and is usually classified in *Ganodermataceae*. The type species, *A. schomburgkii* was described from Guyana. The species of the genus often emerged from the roots of living or dead trees on the ground (Ryvarden 2004), and as traditional circumscription the genus is distributed mainly in Neotropics and tropical or subtropical areas of Africa, Asia and Oceania. The taxonomy of the genus was mostly based on traditional morphological characteristics. Macroscopically, it is usually characterized by annual and stipitate to sessile basidiomata, dull to laccate pilei, fresh pore surface colour changing or not when bruised or dry. Microscopically, the genus presents dimitic to trimitic hyphal system, globose to ellipsoid basidiospores, without truncate apex, which are double-walled with thick and ornamented endospore wall (rarely smooth) (Furtado 1981, Corner 1983, Aime et al. 2003, Ryvarden 2004).

Taxonomic and phylogenetic studies of *Ganodermataceae* have been carried out in recent years, but most studies focused on *Ganoderma* (Smith & Sivasithamparam 2000, Hong & Jung 2004, Pilotti et al. 2004, Wang et al. 2009, Cao et al. 2012, Cao & Yuan 2013, Li et al. 2014b, Lima Júnior et al. 2014, Coetzee et al. 2015, Hapuarachchi et al. 2015, Xing et al. 2016, 2018, Thawthong et al. 2017) and only a few studies dealt with *Amauroderma* (Gomes-Silva et al. 2015, Costa-Rezende et al. 2016, 2017, Song et al. 2016). Regarding this phylogenetic context, *Amauroderma* has been pointed as polyphyletic and regarded as *Amauroderma* s.lat., in which *Amauroderma* s.str. has been defined as a Neotropical clade (Gomes-Silva et al. 2015, Costa-Rezende et al. 2016); as for the relevance of hyphal system composition and basidiospore ultrastructure for generic delimitation in the group was observed, as well as two new genera called *Foraminispora* and *Furtadoa* were proposed (Costa-Rezende et al. 2017). Furthermore, the generic status of *Amauroderma* s.lat. species from Asia and Oceania still was questioned (Song et al. 2016), such as '*Amauroderma rude* clade' composed by *A. rude*, *A. rugosum* and *A. perplexum*; and '*Amauroderma yunnanense* clade' composed by *A. yunnanense* (Costa-Rezende et al. 2017), as well as a variety of Asian and African species which were not phylogenetically tested. In this study, taxonomic and phylogenetic analyses of *Amauroderma* s.lat. were carried out based on more samples from areas outside the neotropics, such as Africa, Asia and Oceania. Based on the abundant specimens, morphological descriptions including ultrastructural features combined with six gene markers provided convincing evidence to clarify the taxonomic status of the species in *Amauroderma* s.lat.

Nine genera are accepted in *Ganodermataceae*, of which *Amauroderma* s.str., *Foraminispora*, *Furtadoa*, *Haddowia* and *Magoderna* have non-truncate basidiospores, while *Ganoderma*, *Tomophagus*, *Humphreya* and *Trachyderma* have basidiospores with obvious truncate apex (Karsten 1881, Imazeki 1939, 1952, Steyaert 1972, Corner 1983, Moncalvo & Ryvarden 1997, Costa-Rezende et al. 2017). *Amauroderma* s.str. is distinguished by di-trimitic hyphal system and endospore wall with solid columnar to semi-reticulated ornamentation (Costa-Rezende et al. 2017). *Foraminispora* has the unique ultrastruc-

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ture features of basidiospores with hollow columnar endospore ornamentation, which persist to the exospore wall forming holes sometimes under SEM (Costa-Rezende et al. 2017). *Furtadoa* is distinguished by a monomitic hyphal system in context, with clamped and simple-septate generative hyphae which are different from other genera (Costa-Rezende et al. 2017). *Haddowia* has distinctive basidiospores, of which the exospore wall with longitudinal ridges partly connected with short transverse walls (Steyaert 1972, Corner 1983). *Magoderna* can be distinguished by woody hard basidiomata with slightly shiny pileus and fibrotic context, and its hyphae in pileal cover anticlinal (Steyaert 1972). *Tomophagus* has light basidiomata, with a pale and soft context (Le et al. 2012). *Humphreya* can be characterized by basidiospores with reticular or erratic irregular ridged double walls (Steyaert 1972). *Trachyderma* is mainly characterized by a fleshy succulent context when growing (Imazeki 1939, 1952).

In this study, in order to clarify the taxonomy and phylogeny of taxa in *Amauroderma* s.lat., specimens from different regions of the world were studied using macro-morphology, microscopic examinations together with ultrastructural observations and molecular phylogenetic analyses of six genes (including ITS, nLSU, *RPB1*, *RPB2*, *TEF* and *TUB*). According to the integrative research, *Amauroderma* s.lat. is divided into four genera including one new genus; furthermore, six new species are described and eight new combinations are proposed and re-described.

MATERIALS AND METHODS

Morphological studies

All samples examined in this study were deposited at the herbaria of the Institute of Microbiology, Beijing Forestry University, China (BJFC), the Institute of Microbiology, Chinese Academy of Sciences, China (HMAS), the Universidade Federal de Pernambuco, Brazil (URM) and the National Herbarium of Victoria, Australia (MEL). Macro-morphological descriptions were based on field notes and herbarium specimens. Special colour terms followed Petersen (1996). Micro-morphological data were obtained from dried specimens and observed under a light microscope following methods in Li et al. (2014a) and Han et al. (2016). Microscopic features and measurements were made from slide preparations stained with Cotton Blue and Melzer's reagent. Spores were measured from sections cut from the tubes. To represent variation in the size of spores, 5 % of measurements were excluded from each end of the range and are given in parentheses. The following abbreviations were used: IKI = Melzer's reagent; IKI– = neither amyloid nor dextrinoid; KOH = 5 % potassium hydroxide; CB = Cotton Blue; CB+ = cyanophilous; L = mean spore length (arithmetic average of all spores); W = mean spore width (arithmetic average of all spores); Q = variation in the L/W ratios between the specimens studied; n (a/b) = number of spores: (a) measured from given number, (b) of specimens. Microscopic features, such as basidiospores, basidia, cystidioles and hyphae, were observed and photographed at a magnification of up to ×1000 with a Nikon Digital Sight DS-Fi2 microscope (Nikon Corporation, Tokyo, Japan), and quantified by the Image-Pro Plus 6.0 software (Media Cybernetics, Silver Spring, USA). Ultrastructures of basidiospores were observed by Scanning Electron Microscopy (SEM) at Beijing Forestry University, China (BJFU) and Tsinghua University, China (THU). Firstly, the fragments of the tubes or spore powder on the pileal surface were slightly broken by Tissue-Prep (Bio-explorer International Limited, Beijing, China) to observe the endospore ornamentation in detail. These tissues were metal sprayed and observed using a Field Emission Scanning Electron Microscope (FESEM) Hitachi SU-8010 (Hitachi, Ltd, Tokyo, Japan).

DNA extraction, amplification and sequencing

A CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd, Beijing, China) and an FH plant DNA kit II (Demeter Biotech Co., Ltd., Beijing, China) were used to extract total genomic DNA from dried specimens and to perform the polymerase chain reaction (PCR) according to the manufacturer's instructions with some modifications (Cui et al. 2019, Shen et al. 2019).

The internal transcribed spacer regions (ITS) was amplified with primer pairs ITS5 and ITS4 (White et al. 1990); for the large subunit of nuclear ribosomal RNA gene (nLSU) we used LR0R and LR5 (Vilgalys & Hester 1990). The primer pairs RPB1-Af and RPB1-Cr (Matheny et al. 2002) were used to amplify the largest subunit of RNA polymerase II (*RPB1*), and primer pairs fRPB2-5F and fRPB2-7CR (Liu et al. 1999) were used to amplify the second subunit of RNA polymerase II (*RPB2*). The translation elongation factor 1-α gene (*TEF*) was amplified with primer pairs EF1-983F and EF1-1567R (Rehner & Buckley 2005). Primer pairs Bt-1a and Bt-1b (Glass & Donaldson 1995) were used to amplify the β-tubulin gene (*TUB*). The primer LR7 (Vilgalys & Hester 1990) was used sometimes as an alternative to LR5; i2.2F and aCr (Binder et al. 2010) were used as alternatives to RPB1-Af and RPB1-Cr; RPB2-6F and bRPB2-7R (Liu et al. 1999) were sometimes used as alternatives to fRPB2-5F and fRPB2-7CR.

The final PCR volume was 30 µl; each tube contained 1 µl each primer, 1 µl extracted DNA, 12 µl ddH_2O and 15 µl 2 × EasyTaq PCR Supermix (TransGen Biotech Co., Ltd., Beijing, China). PCRs were performed on S1000™ Thermal Cycler (Bio-Rad Laboratories, California, USA). The PCR procedure for ITS and *TUB* was: initial denaturation at 95 °C for 3 min, followed by 34 cycles of denaturation at 94 °C for 40 s, annealing at 54 °C for 45 s and extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR procedure for *TEF* was: initial denaturation at 95 °C for 3 min, followed by 34 cycles of denaturation at 94 °C for 40 s, annealing at 55 °C for 45 s and extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR procedure for nLSU was: initial denaturation at 94 °C for 1 min, followed by 34 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 1 min and extension at 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. The PCR procedure for *RPB1* and *RPB2* was an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 1 min, annealing at 55 °C for 2 min and extension at 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. The PCR products were purified and sequenced at the Beijing Genomics Institute (BGI), China, with the same primers. All sequences analysed in this study were deposited at GenBank and listed in Table 1.

Phylogenetic analyses

The sequences generated in this study and retrieved from GenBank were combined with ITS, nLSU, *RPB1*, *RPB2*, *TEF* and *TUB* sequences of *Ganodermataceae* and outgroups. *Perenniporiella chaquenia* and *P. pendula* were selected as outgroups following Costa-Rezende et al. (2016). The datasets were aligned in MAFFT 7 (Katoh & Toh 2008; https://mafft.cbrc.jp/alignment/server/) and manually adjusted in BioEdit (Hall 1999). Two combined matrixes were reconstructed for phylogenetic analyses as a 4-gene dataset (ITS+nLSU+*RPB1*+*TEF*) and a 6-gene dataset (ITS+nLSU+*RPB1*+*RPB2*+*TEF*+*TUB*); their congruences were evaluated with the partition homogeneity test (PHT) by PAUP* v. 4.0b10 (Swofford 2003) under 1 000 homogeneity replicates. The best-fit evolutionary model was selected by hierarchical likelihood ratio tests (hLRT) and Akaike information criterion (AIC) in MrModeltest2 v. 2.3 (Nylander 2008) after scoring 24 models of evolution by PAUP* v. 4.0b10. The maximum likelihood (ML) and Bayesian Inference (BI)

Table 1 Taxa information and GenBank accession numbers of the sequences used in this study.

Species	Voucher	GenBank accession No.					
		ITS	nLSU	*RPB1*	*RPB2*	*TEF*	*TUB*
Amauroderma aurantiacum	FLOR 52205	KR816510	KU315205	–	–	–	–
	DHCR540 (HUEFS)	MF409961	MF409953	MF436687	–	–	–
A. calcigenum	FLOR 52315	KR816514	–	–	–	–	–
	URM86847	KT006601	–	–	–	–	–
	URM83864	JX982565	–	–	–	–	–
	URM89213	MK119792[a]	MK119870[a]	–	MK121484[a]	MK121541[a]	MK124977[a]
	URM89215	MK119793[a]	MK119871[a]	–	MK121485[a]	MK121542[a]	–
A. calcitum	FLOR 50931/DHCR538 (HUEFS)	KR816528	KU315207	MF436690	–	–	–
	FLOR 52230	KR816529	–	–	–	–	–
A. camerarium	FLOR 52169	KR816523	–	–	–	–	–
	FLOR 52216	KR816509	–	–	–	–	–
A. elegantissimum	URM82789	JX310844	KT006617	–	–	–	–
	URM82787	JX310843	KT006616	–	–	–	–
	Dai 17431	MK119794[a]	MK119872[a]	–	MK121493[a]	MK121543[a]	MK124978[a]
	URM83822	MK119795[a]	MK119873[a]	–	MK121494[a]	MK121544[a]	–
A. exile	URM82794	JX310845	–	–	–	–	–
	URM89226	MK119796[a]	MK119874[a]	–	–	MK121545[a]	–
A. intermedium	GAS910 (HUEFS)	MF409959	–	MF436685	–	–	–
	FLOR 52248	KR816527	KU315209	–	–	–	–
A. laccatostipitatum	URM83238	JX310847	–	–	–	–	–
	HFSL ACGS7	KT006602	–	–	–	–	–
	URM89240	MK119797[a]	MK119875[a]	–	MK121489[a]	MK121546[a]	MK124979[a]
A. omphalodes	DHCR499/501 (HUEFS)	MF409956	MF409951	MF436682	–	MF421238	–
	DHCR500 (HUEFS)	MF409957	MF409952	MF436683	–	MF421239	–
	URM89247	–	MK119876[a]	–	MK121488[a]	MK121547[a]	–
	URM86852	MK119798[a]	MK119877[a]	–	–	MK121548[a]	–
A. praetervisum	URM84230	KC348461	–	–	–	–	–
	URM84223	KT006605	–	–	–	–	–
	URM87611	KT006606	–	–	–	–	–
	Dai 17385	MK119799[a]	–	–	–	MK121549[a]	MK124980[a]
	URM87687	MK119800[a]	MK119878[a]	–	MK121487[a]	MK121550[a]	–
	URM89233	MK119801[a]	MK119879[a]	–	MK121486[a]	MK121551[a]	MK124981[a]
A. schomburgkii	URM83228	JX310848	–	–	–	–	–
	URM89271	MK119802[a]	MK119880[a]	–	MK121495[a]	MK121552[a]	–
	URM89272	MK119803[a]	MK119881[a]	–	MK121496[a]	MK121553[a]	–
	URM89273	MK119804[a]	MK119882[a]	–	MK121497[a]	MK121554[a]	MK124982[a]
	URM89225	MK119805[a]	MK119883[a]	–	MK121498[a]	MK121555[a]	MK124983[a]
A. subsessile	URM83905	JX982570	MK119884[a]	–	–	–	–
	URM89293	MK119806[a]	MK119885[a]	–	MK121490[a]	MK121556[a]	MK124984[a]
	URM89294	MK119807[a]	MK119886[a]	–	MK121491[a]	MK121557[a]	MK124985[a]
	URM89295	MK119808[a]	MK119887[a]	–	MK121492[a]	MK121558[a]	MK124986[a]
Foraminispora austrosinensis	Cui 16425	MK119809[a]	MK119888[a]	–	–	MK121559[a]	MK124987[a]
	Cui 14318	MK119810[a]	MK119889[a]	–	–	MK121560[a]	–
	Cui 14319	MK119811[a]	MK119890[a]	–	–	–	–
Fo. concentrica	Cui 12644	MK119812[a]	MK119891[a]	–	MK121499[a]	MK121561[a]	–
	Cui 12646	MK119813[a]	MK119892[a]	–	MK121500[a]	MK121562[a]	–
	Cui 12647	MK119814[a]	MK119893[a]	–	MK121503[a]	MK121563[a]	–
	Cui 12648	MK119815[a]	MK119894[a]	–	MK121501[a]	MK121564[a]	–
	Cui 16238	MK119816[a]	MK119895[a]	–	MK121504[a]	MK121565[a]	MK124988[a]
	Cui 16239	MK119817[a]	MK119896[a]	–	MK121506[a]	MK121566[a]	MK124989[a]
	Cui 16240	MK119818[a]	MK119897[a]	–	MK121505[a]	MK121567[a]	–
	Cui 16510	MK119819[a]	MK119898[a]	–	MK121502[a]	MK121568[a]	–
Fo. rugosa	FLOR 52191	KU315200	KU315216	–	–	–	–
	DHCR512 (HUEFS)	MF409960	–	MF436686	–	MF421240	–
	DHCR554 (HUEFS)	MF409962	MF409954	MF436688	–	–	–
	DHCR560 (HUEFS)	MF409963	MF409955	MF436689	–	MF421241	–
	URM89290	MK119820[a]	MK119899[a]	–	–	MK121569[a]	–
Fo. yinggelingensis	Cui 13618	MK119821[a]	MK119900[a]	–	MK121536[a]	MK121570[a]	–
	Cui 13630	MK119822[a]	MK119901[a]	–	–	–	–
Fo. yunnanensis	Cui 7974	KJ531653	KU220013	–	–	–	–
	Dai 13021	KJ531654	–	–	–	–	–
	Yuan 2253	KJ531655	–	–	–	–	–
Furtadoa brasiliensis	URM83578	JX310841	–	–	–	–	–
	TBG58	JX982569	–	–	–	–	–
Fu. biseptata	FLOR 50932	KU315196	KU315206	–	–	–	–
Ganoderma annulare	KCTC 16803	JQ520160	–	–	–	–	JQ675613
G. applanatum	Wei 5787a	KF495001	KF495011	–	–	KF494978	–
	Dai 12483	KF494999	KF495009	–	–	KF494977	–
G. aridicola	Dai 12588	KU572491	–	–	–	KU572502	–

Table 1 (cont.)

Species	Voucher	GenBank accession No.					
		ITS	nLSU	*RPB1*	*RPB2*	*TEF*	*TUB*
G. australe	DHCR411 (HUEFS)	MF436675	MF436672	MF436680	–	MF436677	–
	DHCR417 (HUEFS)	MF436676	MF436673	MF436681	–	MF436678	–
G. boninense	WD 2085	KJ143906	–	KJ143945	–	KJ143925	–
	WD 2028	KJ143905	KU220015	KJ143944	–	KJ143924	–
G. chalceum	URM80457	JX310812	JX310826	–	–	–	–
G. curtisii	CBS 100132	JQ520164	–	KJ143947	KJ143967	KJ143927	JQ675617
	CBS 100131	JQ781848	–	KJ143946	KJ143966	KJ143926	–
G. ecuadorense	URM89440	–	MK119906[a]	–	MK121533[a]	MK121575[a]	MK124994[a]
	URM89441	MK119827[a]	MK119907[a]	–	MK121534[a]	MK121576[a]	MK124995[a]
	URM89449	MK119828[a]	MK119908[a]	–	MK121535[a]	MK121577[a]	MK124996[a]
G. enigmaticum	Dai 15970	KU572486	–	–	–	KU572496	–
	Dai 15971	KU572487	–	–	–	KU572497	–
G. gibbosum	KUT 0805	AB733121	AB733303	–	–	–	–
G. hoehnelianum	Dai 11995	KU219988	KU220016	–	MG367497	MG367550	–
	Cui 13982	MG279178	–	–	MG367515	MG367570	–
G. leucocontextum	Dai 15601	KU572485	–	–	–	KU572495	–
G. lingzhi	Dai 12574	KJ143908	–	JX029985	JX029981	JX029977	–
	Cui 9166	KJ143907	–	JX029982	JX029978	JX029974	–
G. lobatum	JV 1212/10J	KF605676	–	–	–	KU572501	–
G. lucidum	K 175217	KJ143911	–	KJ143950	KJ143971	KJ143929	–
	Cui 9207	KJ143910	–	KJ143949	KJ143970	KJ143928	–
G. meredithae	ASI 7140	JQ520191	–	–	–	–	JQ675644
	ATCC 64492	JQ520190	–	–	–	–	JQ675643
G. multipileum	Dai 9447	KJ143914	–	KJ143953	KJ143973	KJ143932	–
	CWN 04670	KJ143913	–	KJ143952	KJ143972	KJ143931	–
G. multiplicatum	Dai 12320	KU572490	–	–	–	KU572500	–
	Dai 13710	KU572489	–	–	–	KU572499	–
G. orbiforme	URM83334	JX310814	JX310828	–	–	–	–
	URM83336	JX310816	JX310830	–	–	–	–
	URM86213	MK119829[a]	MK119909[a]	–	–	MK121578[a]	–
G. oregonense	CBS 266.88	JQ781876	–	KJ143955	KJ143975	–	–
	CBS 265.88	JQ781875	–	KJ143954	KJ143974	KJ143933	–
G. parvulum	URM83345	JX310820	JX310834	–	–	–	–
	URM80765	JX310822	JX310836	–	–	–	–
G. perzonatum	SP445985	KJ792745	–	–	–	–	–
	SP445987	KJ792747	–	–	–	–	–
	URM89437	MK119830[a]	–	–	–	MK121579[a]	–
G. ramosissimum	xsd08032	EU918700	–	–	–	–	–
	xsd08085	FJ478127	–	–	–	–	–
G. resinaceum	CBS 194.76	X78737/ X78758	–	KJ143956	–	KJ143934	–
	BR 4150	KJ143915	–	KJ143957	–	–	–
G. sessile	JV 1209/9	KF605629	–	KJ143958	–	KJ143936	–
	JV 1209/27	KF605630	–	KJ143959	KJ143976	KJ143937	–
G. sichuanense	CGMCC5.533	JN197284	–	–	JN197290	–	–
	HMAS130128	JF915404	–	–	–	–	–
G. sinense	Wei 5327	KF494998	KF495008	–	–	KF494976	–
G. sp.	GD026 (HUEFS)	MF436674	MF436671	MF436679	–	–	–
G. subamboinense	GSUB136	DQ425005	–	–	–	–	DQ288096
	GSUB137	DQ425006	–	–	–	–	DQ288097
G. tornatum	URM82776	JQ514110	JX310800	–	–	–	–
	TBG01AM2009	JQ514108	JX310808	–	–	–	–
G. tsugae	AFTOL-ID 771	DQ206985	AY684163	–	DQ408116	DQ059048	–
	Dai 12760	KJ143920	–	KJ143961	KJ143978	KJ143940	–
G. zonatum	FL-03	KJ143922	–	–	KJ143980	KJ143942	–
	FL-02	KJ143921	–	KJ143962	KJ143979	KJ143941	–
Haddowia longipes	LPDR17072708	MK345423	MK346828				
	LPDR17072709	MK345424	MK346829				
Humphreya coffeata	FLOR 50933	KU315204	–	–	–	–	–
Magoderna subresinosum	Dai 18626	MK119823[a]	MK119902[a]	–	MK121507[a]	MK121571[a]	MK124990[a]
	Dai 18630	MK119824[a]	MK119903[a]	–	MK121510[a]	MK121572[a]	MK124991[a]
	Dai 18634	MK119825[a]	MK119904[a]	–	MK121508[a]	MK121573[a]	MK124992[a]
	Dai 18639	MK119826[a]	MK119905[a]	–	MK121509[a]	MK121574[a]	MK124993[a]
Sanguinoderma bataanense	Cui 6285	MK119831[a]	MK119910[a]	–	MK121537[a]	MK121580[a]	MK124997[a]
	Dai 10746	MK119832[a]	MK119911[a]	–	MK121511[a]	MK121581[a]	–
S. elmerianum	Cui 8940	MK119833[a]	MK119912[a]	–	–	–	–
	HMAS 133187	MK119834[a]	MK119913[a]	–	–	–	–

Table 1 (cont.)

Species	Voucher	GenBank accession No.					
		ITS	nLSU	*RPB1*	*RPB2*	*TEF*	*TUB*
S. flavovirens	Cui 16935	–	MK119914[a]	MK119858[a]	MK121532[a]	MK121582[a]	MK124998[a]
S. laceratum	Cui 8155	MK119851[a]	MK119928[a]	–	–	–	–
S. microporum	Cui 8898	–	MK119932[a]	–	–	–	–
	Cui 13851	MK119854[a]	MK119933[a]	–	MK121512[a]	MK121602[a]	–
	Cui 14001	MK119855[a]	MK119934[a]	–	MK121513[a]	MK121603[a]	–
	Cui 14022	MK119856[a]	MK119935[a]	–	MK121515[a]	MK121604[a]	–
	Cui 16335	MK119857[a]	MK119936[a]	–	MK121514[a]	MK121605[a]	MK125013[a]
	Cui 16336	–	MK119937[a]	–	–	MK121606[a]	–
	Cui 16338	–	MK119938[a]	–	–	MK121607[a]	–
S. perplexum	Cui 6496	KJ531650	KU220001	–	MK121538[a]	MK121583[a]	–
	Dai 10811	KJ531651	KU220002	–	MK121539[a]	MK121584[a]	–
	Cui 6554	MK119835[a]	MK119915[a]	MK119859[a]	MK121540[a]	MK121585[a]	–
S. reniforme	Cui 16511	MK119850[a]	MK119929[a]	MK119867[a]	MK121531[a]	MK121599[a]	MK125010[a]
S. rude	Cui 16592	MK119836[a]	MK119916[a]	MK119860[a]	MK121521[a]	MK121586[a]	–
	MEL 2362204	MK119837[a]	MK119917[a]	MK119861[a]	MK121522[a]	MK121587[a]	MK124999[a]
	MEL 2150776	MK119838[a]	MK119918[a]	–	–	MK121588[a]	–
	MEL 2335651	MK119839[a]	MK119919[a]	–	–	MK121589[a]	MK125000[a]
	MEL 2231602	MK119840[a]	MK119920[a]	MK119862[a]	MK121523[a]	MK121590[a]	MK125001[a]
	MEL 2028873	MK119841[a]	MK119921[a]	MK119863[a]	MK121526[a]	MK121591[a]	MK125002[a]
	MEL 2317411	MK119842[a]	–	MK119864[a]	MK121524[a]	MK121592[a]	MK125003[a]
S. rugosum	Cui 8795	MK119843[a]	MK119922[a]	MK119865[a]	MK121516[a]	MK121593[a]	MK125004[a]
	Cui 9011	KJ531664	KU220010	–	MK121517[a]	KU572504	–
	Cui 9012	KJ531665	KU220011	–	MK121518[a]	KU572503	–
	Cui 16337	MK119844[a]	MK119923[a]	–	MK121519[a]	MK121594[a]	MK125005[a]
	Cui 16166	MK119845[a]	MK119924[a]	MK119866[a]	MK121520[a]	MK121595[a]	MK125006[a]
S. sinuosum	MEL 2366586	MK119852[a]	MK119930[a]	MK119868[a]	MK121527[a]	MK121600[a]	MK125011[a]
	MEL 2341763	MK119853[a]	MK119931[a]	MK119869[a]	MK121525[a]	MK121601[a]	MK125012[a]
S. sp.	Dai 18148	MK119846[a]	MK119925[a]	–	MK121528[a]	MK121596[a]	MK125007[a]
	Dai 18149	MK119847[a]	MK119926[a]	–	MK121529[a]	MK121597[a]	MK125008[a]
	Dai 18151	MK119848[a]	–	–	MK121530[a]	MK121598[a]	MK125009[a]
	URM450213	MK119849[a]	MK119927[a]	–	–	–	–
Tomophagus cattienensis	CT119	JN184398	–	–	–	–	–
	CT99	JN184397	–	–	–	–	–
T. colossus	TC-02	KJ143923	–	KJ143963	–	KJ143943	–
	URM80450	JX310825	JX310839	–	–	–	–
	URM83330	JQ618247	JX310811	–	–	–	–
Trachyderma tsunodae	GR363	FJ154773	–	–	–	–	–
	WD2034	AB588989	AB368069	–	AB368127	–	–
Perenniporiella chaquenia	MUCL 49758	NR111365	FJ393857	–	–	HM467602	–
P. pendula	MUCL 47129	FJ411082	FJ393854	–	–	HM467600	–

[a] Newly generated sequences for this study.
Bold species = new species.

analyses were performed based on the two datasets respectively. Settings for phylogenetic analyses followed Song & Cui (2017) and Zhu et al. (2019). ML researches were conducted with RAxML-HPC v. 8.2.3 (Stamatakis 2014) involved 1 000 ML searches under the GTRGAMMA model, and only the maximum likelihood best tree from all searches was kept. In addition, 1 000 rapid bootstrap replicates were run with the GTRCAT model to assess ML bootstrap values (ML) of the nodes. BI were performed using MrBayes v. 3.2 (Ronquist & Huelsenbeck 2003) with four simultaneous independent chains for two datasets, performing 10 million generations until the split deviation frequency value < 0.01, and sampled every 100th generation. The first 25 % sampled trees were discarded as burn-in, while the remaining ones were used to calculate Bayesian posterior probabilities (BPP) of the clades. The ML bootstrap (ML) ≥ 50 % and Bayesian posterior probabilities (BPP) ≥ 0.95 were presented on topologies from ML analyses, respectively. All trees were viewed in FigTree v. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). The final alignments and the retrieved topologies were deposited in TreeBASE (http://www.treebase.org), under accession ID: 24765 (http://purl.org/phylo/treebase/phylows/study/TB2:S24765).

RESULTS

Molecular phylogeny

In this study, 545 sequences derived from six gene loci (ITS, nLSU, *RPB1*, *RPB2*, *TEF* and *TUB*) were used to reconstruct phylogenetic trees of *Ganodermataceae*, 308 of them were newly generated, including 66 sequences of ITS, 69 of nLSU, 12 of *RPB1*, 57 of *RPB2*, 67 of *TEF*, and 37 of *TUB*. The phylogenetic reconstruction performed with maximum likelihood (ML) and Bayesian inference (BI) analyses for two combined datasets showed similar topology and few differences in statistical support. The partition homogeneity test indicated all the six different genes display a congruent phylogenetic signal (P value = 1.00). The best-fit evolutionary model selected by MrModeltest2 v. 2.3 for each region of six genes were HKY+I+G (ITS1), K80 (5.8S), HKY+I+G (ITS2), GTR+I+G (nLSU), HKY+G (*RPB1* introns), F81 (*RPB1* 1st codon), GTR+G (*RPB1* 2nd codon), GTR+G (*RPB1* 3rd codon), SYM+G (*RPB2* introns), K80+I+G (*RPB2* 1st codon), GTR+I+G (*RPB2* 2nd codon), GTR+I+G (*TEF* introns), HKY+I+G (*TEF* 1st codon), SYM+I+G (*TEF* 2nd codon), GTR+G (*TEF* 3rd codon) and HKY+I+G (*TUB*). These models were applied in Bayesian analyses for two combined datasets.

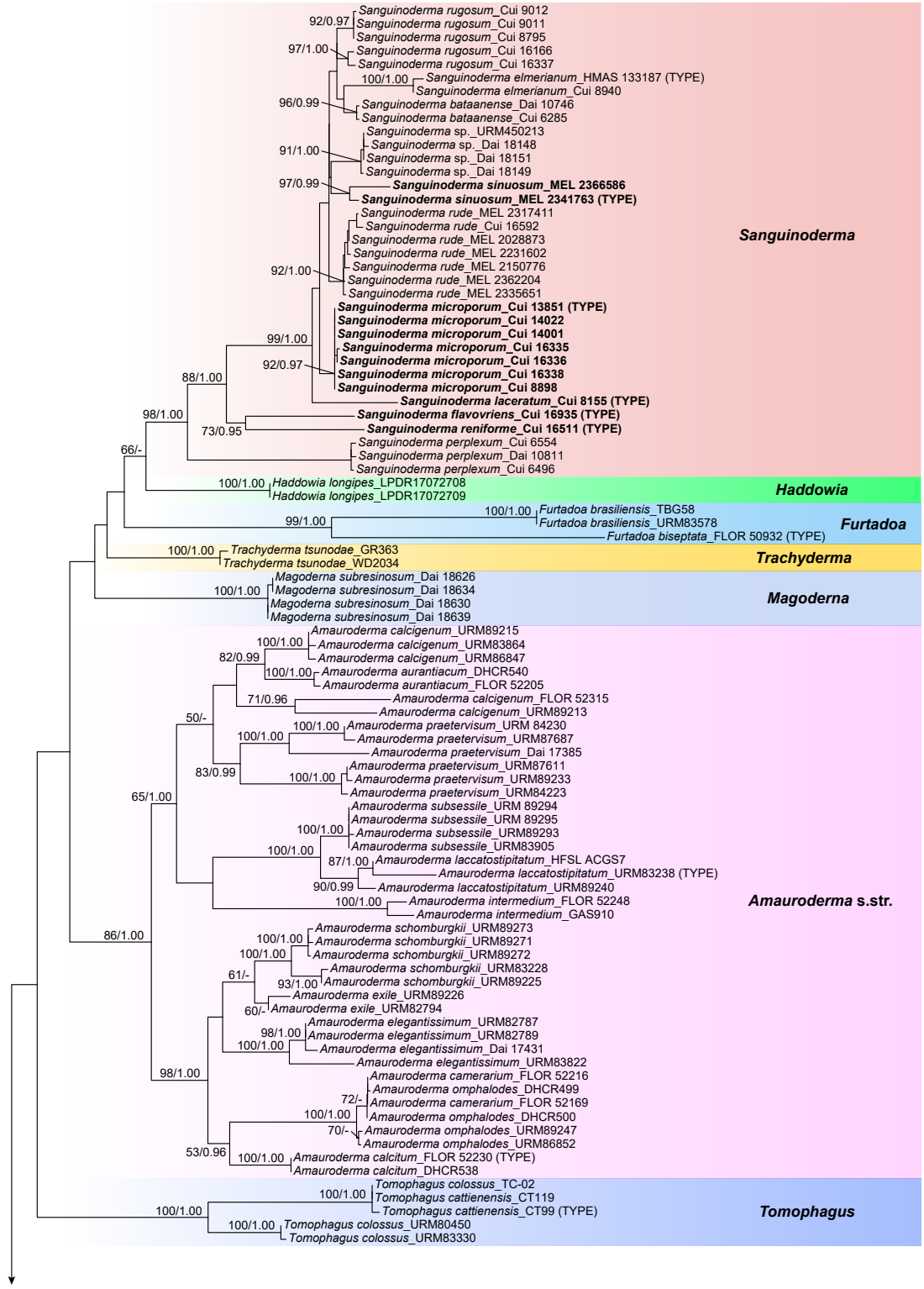

Fig. 1 ML analyses of *Ganodermataceae* based on dataset of ITS+nLSU+*RPB1*+*TEF*. ML bootstrap values higher than 50 % and Bayesian posterior probabilities values more than 0.95 are shown. New species are in **bold**.

The combined 4-gene dataset (ITS+nLSU+*RPB1*+*TEF*) included sequences from 175 specimens representing 69 taxa of *Ganodermataceae* and *Perenniporiella chaquenia* and *P. pendula* as outgroups. The dataset had an aligned length of 3 354 characters, of which 2 366 were constant, 196 were variable and parsimony-uninformative, and 792 were parsimony-informative. The average standard deviation of split frequencies in the Bayesian analyses reached 0.008332. The calculated values based on the dataset are shown in Fig. 1. The clades obtained in this topology, besides the outgroup, were *Amauroderma* s.str. (86 % ML, 1.00 BPP), *Foraminispora* (83 % ML, 0.99 BPP), *Furtadoa* (99 % ML, 1.00 BPP), *Ganoderma*, *Haddowia* (100 % ML, 1.00 BPP), *Humphreya*, *Magoderna* (100 % ML, 1.00 BPP), *Sanguinoderma* (98 % ML, 1.00 BPP), *Tomophagus* (100 % ML, 1.00 BPP) and *Trachyderma* (100 % ML, 1.00 BPP).

The combined 6-gene dataset (ITS+nLSU+*RPB1*+*RPB2*+ *TEF*+*TUB*) also included sequences from 175 specimens representing 69 taxa of *Ganodermataceae* and *Perenniporiella chaquenia* and *P. pendula* as outgroups. The dataset had an aligned length of 4 810 characters, of which 3 168 were constant, 256 were variable and parsimony-uninformative, and 1 386 were parsimony-informative. The average standard deviation of split frequencies in the Bayesian analyses reached 0.009067. The calculated values based on the dataset are shown in Fig. 2.

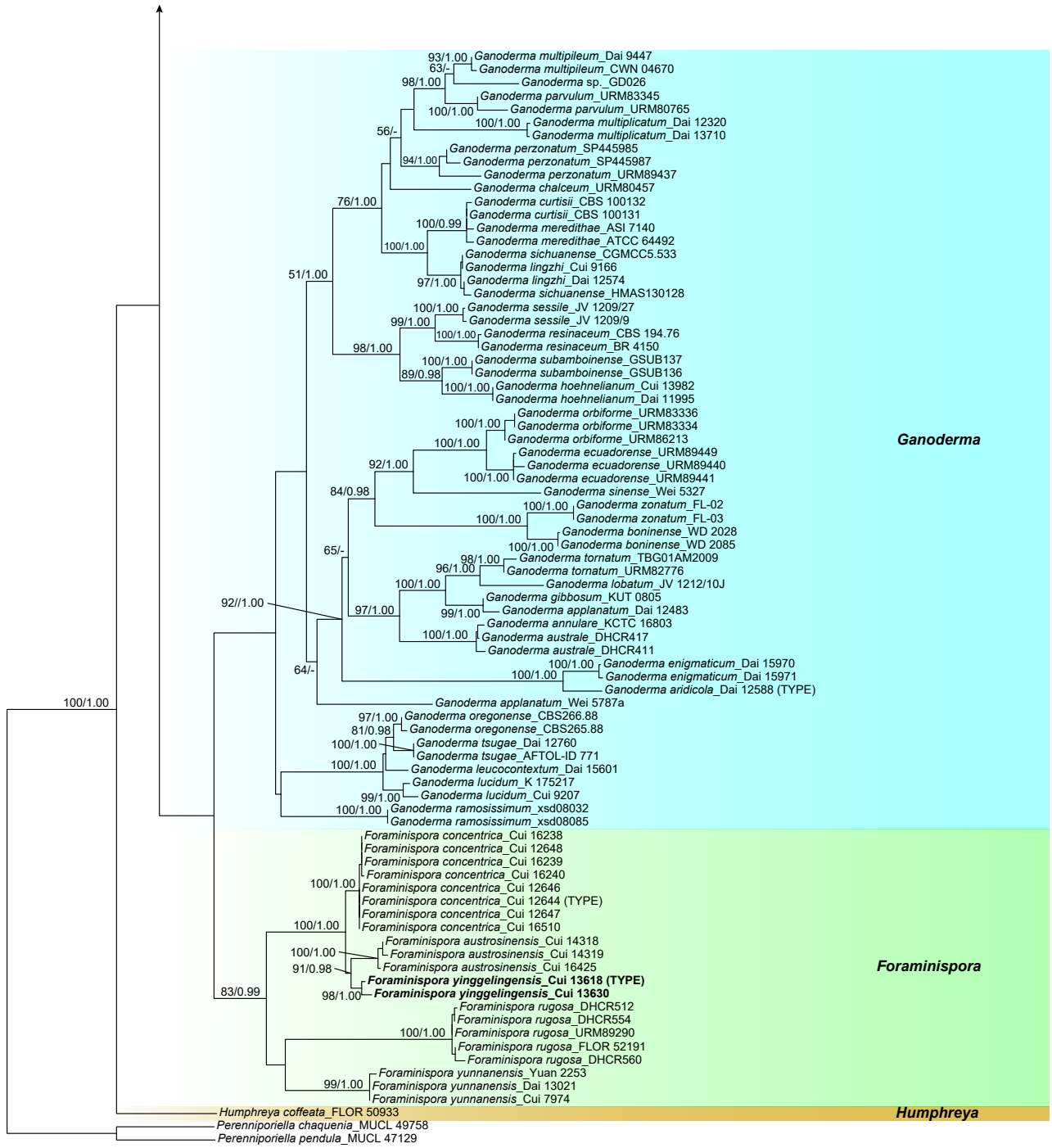

Fig. 1 (cont.)

The clades obtained in this topology were *Amauroderma* s.str. (89 % ML, 1.00 BPP), *Foraminispora* (77 % ML, 0.98 BPP), *Furtadoa* (99 % ML, 1.00 BPP), *Ganoderma*, *Haddowia* (100 % ML, 1.00 BPP), *Humphreya*, *Magoderna* (100 % ML, 1.00 BPP), *Sanguinoderma* (99 % ML, 1.00 BPP), *Tomophagus* (100 % ML, 1.00 BPP) and *Trachyderma* (100 % ML, 1.00 BPP).

The phylogenetic trees (Fig. 1, 2) show that the species of *Amauroderma* s.lat. are divided into four distinct clades:

The *Amauroderma* s.str. clade: All species in this clade were derived from neotropical areas, including *A. aurantiacum*, *A. calcigenum*, *A. calcitum*, *A. camerarium*, *A. elegantissimum*, *A. exile*, *A. intermedium*, *A. laccatostipitatum*, *A. omphalodes*, *A. praetervisum*, *A. schomburgkii* and *A. subsessile*.

The *Foraminispora* clade: Previously, only one species, *Fo. rugosa,* from the Neotropics was included in this clade. According to our study, one new species: *Fo. yinggelingensis*, and three new combinations: *Fo. austrosinensis*, *Fo. concentrica* and *Fo. yunnanensis* from East Asia are also included in this clade.

The *Furtadoa* clade: Two species: *Fu. biseptata* and *Fu. brasiliensis* from the Neotropics clustered in this clade.

The *Sanguinoderma* clade: The species in this clade were mainly found in warm temperate to subtropical or tropical regions of Asia, Africa and Oceania rather than the Neotropics. Until now, this clade included five new species: *S. flavovirens*, *S. laceratum*, *S. microporum*, *S. reniforme* and *S. sinuosum*; five new combinations: *S. bataanense*, *S. elmerianum*, *S. perplexum*, *S. rude* and *S. rugosum*; and one undetermined taxon: *Sanguinoderma* sp.

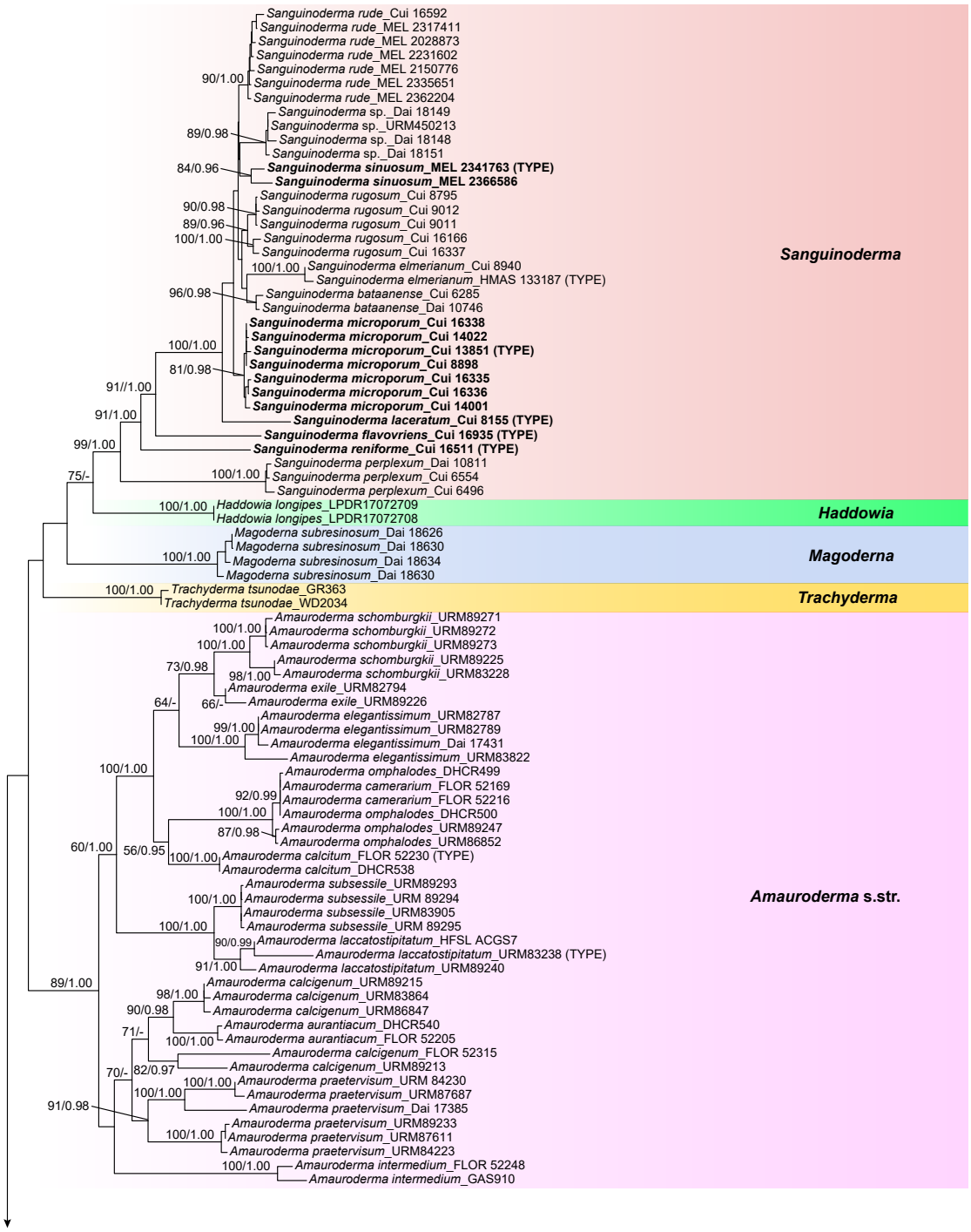

Fig. 2 ML analyses of *Ganodermataceae* based on dataset of ITS+nLSU+*RPB1*+*RPB2*+*TEF*+*TUB*. ML bootstrap values higher than 50 % and Bayesian posterior probabilities values more than 0.95 are shown. New species are in **bold**.

TAXONOMY

Key to genera of Amauroderma s.lat.

1. Fresh pore surface colour changing to blood red when bruised . . . . . *Sanguinoderma*
1. Fresh pore surface colour unchanging when bruised . . . 2
2. Pileal surface dull, tomentose, yellowish brown to reddish brown . . . . . *Foraminispora*
2. Pileal surface dull to laccate, glabrous to tomentose, dark brown 3
3. Pileal surface dull to laccate; hyphal system dimitic in the context, generative hyphae clamped . *Amauroderma* s.str.
3. Pileal surface dull; hyphal system monomitic in the context, generative hyphae clamped to simple-septate . . *Furtadoa*

Amauroderma s.str. Murrill, Bull. Torrey Bot. Club 32: 366. 1905 — MycoBank MB17052

Type species. *Amauroderma schomburgkii* (Mont. & Berk.) Torrend, Brotéria, Sér. Bot. 18 (no. 2): 140. 1920.

Basidiomata annual, centrally or laterally stipitate to sessile or subsessile, coriaceous, corky to woody hard. Pileus single, fan-shaped, suborbicular or funnel-shape. Pileal surface in shades of dark brown, vinaceous brown to almost black, dull, glittery or laccate, glabrous to tomentose, concentrically zonate or furrowed. Pore surface pale white, yellowish brown, orange or brown when dry, colour unchanging when bruised; pores circular to angular. Context pale white, yellowish brown, pinkish brown, brown, corky. Hyphal system dimitic; generative hyphae colourless, with clamp connections, thin-walled; skeletal hyphae

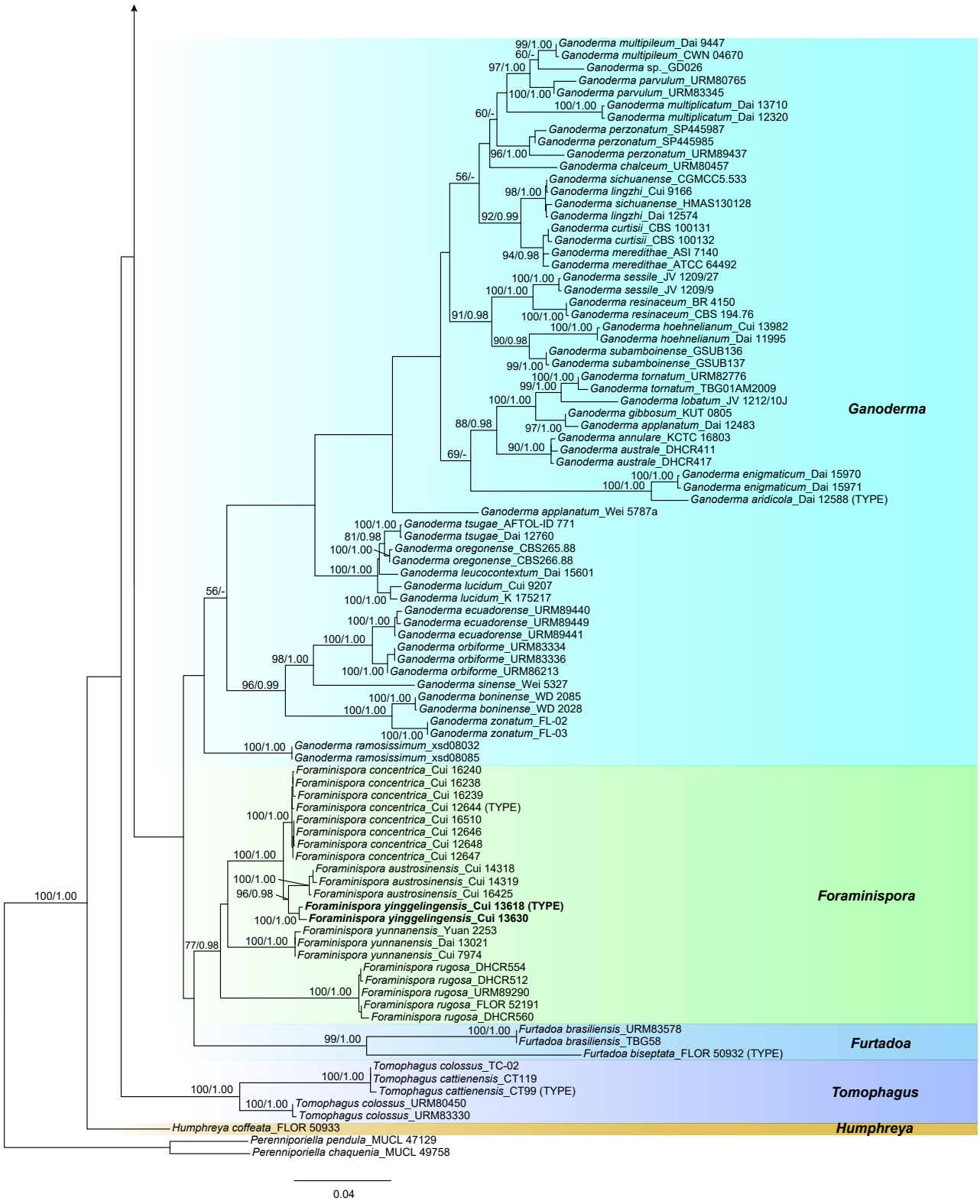

Fig. 2 (cont.)

colourless to pale yellow to brown, thick-walled, arboriform. Basidiospores globose or ellipsoid to obovoid, colourless to pale yellow, double-walled, endospore wall smooth or ornamented, IKI– or dextrinoid.

Notes — So far, all species in *Amauroderma* s.str. are from the Neotropics and they are morphologically variable. The geographical distribution and the combination of morphological characteristics, such as a colour-unchanging pore surface when bruised, presence of skeletal hyphae in both context and tubes, basidiospores with solid columnar endospore ornamentation can be used to distinguish this genus from other genera of *Amauroderma* s.lat. Based on morphological characteristics, 24 species were included in *Amauroderma* s.str., of which 14 have DNA sequences. *Amauroderma trichodematum* presents a monomitic hyphal system and is probably related to *Furtadoa* (Robledo et al. 2015). Since this feature is not in accordance with the current circumscription of *Amauroderma* s.str., this species was not included in this key.

Key to accepted species of Amauroderma s.str.

1. Pileal surface laccate . . . . . *A. renidens*
1. Pileal surface non-laccate 2
2. Basidiomata with a laccate stipe 3
2. Basidiomata without a laccate stipe 4
3. Pores angular, 7–8 per mm; basidiospores 8–10 × 7–8 µm . . . . . *A. laccatostipitatum*
3. Pores circular, 5–6 per mm; basidiospores 9–11 × 7–8 µm . . . . . *A. picipes*
4. Basidiomata sessile to substipitate 5
4. Basidiomata distinctly stipitate 6
5. Basidiomata sessile, pileal surface azonate, pores angular . . . . . *A. sessile*
5. Basidiomata substipitate, pileal surface zonate, pores circular . . . . . *A. subsessile*
6. Stipe white . . . . . *A. albostipitatum*
6. Stipe different coloured 7
7. Pileus with 2–9 lobes . . . . . *A. floriformum*
7. Pileus entire 8
8. Basidiospores with smooth inner layer . . *A. coltricioides*
8. Basidiospores with ornamented inner layer 9
9. Context white to cream 10
9. Context cinnamon to dark brown 11
10. Pileal surface tomentose, pores 3–4 per mm; basidiospores 7–10 × 7–9 µm . . . . . *A. boleticeum*
10. Pileal surface glabrous, pores 1–3 per mm; basidiospores 10–13 × 8–10 µm . . . . . *A. partitum*
11. Pileus ≤ 2 mm thick, context without black lines . . . . . *A. elegantissimum*
11. Pileus > 2 mm thick, context with or without black lines 12
12. Basidiospores distinctly dextrinoid 13
12. Basidiospores non-dextrinoid 14
13. Pores 4–6 per mm; basidiospores obovoid *A. ovisporum*
13. Pores 7–8 per mm; basidiospores globose to subglobose . . . . . *A. unilaterum*
14. Basidiomata woody hard; basidiospores oblong, 6–7.5 µm wide . . . . . *A. oblongisporum*
14. Basidiomata corky to woody hard; basidiospores globose to ellipsoid, > 7.5 µm wide 15
15. Pores ≤ 3 per mm 16
15. Pores > 3 per mm 19
16. Basidiomata woody hard; basidiospores 9–11 µm long . . . . . *A. intermedium*
16. Basidiomata corky; basidiospores > 11 µm long 17
17. Pileal surface slightly shiny; basidiospores with slightly ornamented inner layer . . . . . *A. calcitum*
17. Pileal surface dull; basidiospores with distinctly ornamented inner layer 18
18. Basidiospores globose to subglobose, 14–17 × 13–17 µm . . . . . *A. aurantiacum*
18. Basidiospores broadly ellipsoid to ellipsoid, 13.5–16 × 10–12 µm . . . . . *A. calcigenum*
19. Context without black lines 20
19. Context with black lines 21
20. Pileal surface yellowish brown, pores 5–7 per mm; basidiospores broadly ellipsoid . . . . . *A. camerarium*
20. Pileal surface reddish brown, pores 3–5 per mm; basidiospores globose to subglobose . . . . . *A. pseudoboletus*
21. Basidiomata coriaceous to corky, pileal surface slightly shiny . . . . . *A. exile*
21. Basidiomata woody hard, pileal surface dull 22
22. Pore surface pale white; basidiospores pale yellow . . . . . *A. schomburgkii*
22. Pore surface cinnamon; basidiospores yellow to yellowish brown 23
23. Basidiospores distinctly thick-walled, with distinctly ornamented inner layer . . . . . *A. omphalodes*
23. Basidiospores medially thick-walled, with faintly ornamented inner layer . . . . . *A. praetervisum*

Foraminispora Robledo, D.H. Costa & Drechsler-Santos, Persoonia 39: 258. 2017 — MycoBank MB819015

Type species. *Foraminispora rugosa* (Berk.) D.H. Costa, Drechsler-Santos & Robledo, Persoonia 39: 262. 2017.

Basidiomata annual, centrally to laterally stipitate, corky to woody hard. Pileus single, suborbicular to umbelliform. Pileal surface yellowish brown to reddish brown, dull, tomentose, concentrically zonate or furrowed, radially rugose. Pore surface white to straw colour when dry, colour unchanging when bruised; pores circular to angular; dissepiments thin to thick, entire. Context white to pale yellow, without dark resinous lines, corky. Hyphal system dimitic to trimitic; all hyphae IKI–, CB+; tissues darkening in KOH; generative hyphae colourless, thin-walled, with clamp connections; skeletal hyphae colourless to pale yellow, thick-walled, arboriform branched and flexuous; binding hyphae colourless, subsolid, branched and flexuous. Basidiospores globose to ellipsoid, colourless to pale yellow, double and distinctly thick-walled, exospore wall uneven or foveolate, endospore wall with hollow and columnar spinules which persist until the exospore wall forming holes visible under SEM, IKI– or slightly dextrinoid, CB+.

Notes — *Foraminispora* was established by Costa-Rezende et al. (2017) and only *Fo. rugosa* from the Neotropics was included. In our current study, three taxa previously belonging to *Amauroderma* s.lat. and one new species grouped together with *Fo. rugosa* and formed the *Foraminispora* clade in both the 4-gene and 6-gene based phylogenetic analyses (Fig. 1, 2). All these five species share similar spore ultrastructural characters such as uneven exospore wall with holes causing by hollow and columnar spinules on endospore wall which are unique within *Ganodermataceae* (Fig. 3).

Key to accepted species of Foraminispora

1. Basidiospores > 10 µm long 2
1. Basidiospores < 10 µm long 3
2. Pores 2–3 per mm, dissepiments lacerate . . . . . *Fo. yunnanensis*
2. Pores 5–8 per mm, dissepiments entire . . . . . *Fo. rugosa*
3. Pores 3–5 per mm; basidiospores subglobose to broadly ellipsoid . . . . . *Fo. concentrica*
3. Pores > 5 per mm; basidiospores globose to subglobose . 4
4. Basidiomata corky; cystidioles clavate, basidiospores IKI– . . . . . *Fo. austrosinensis*
4. Basidiomata woody hard; cystidioles absent, basidiospores slightly dextrinoid . . . . . *Fo. yinggelingensis*

Foraminispora austrosinensis (J.D. Zhao & L.W. Hsu) Y.F. Sun & B.K. Cui, *comb. nov*. — MycoBank MB828440; Fig. 3a–b, 4

Basionym. *Amauroderma austrosinense* J.D. Zhao & L.W. Hsu, Acta Mycol. Sin. 3(1): 20. 1984.

Basidiomata annual, centrally to laterally stipitate, coriaceous to corky. Pileus single, suborbicular to umbelliform, up to 8.5 cm diam and 5 mm thick. Pileal surface yellow to yellowish

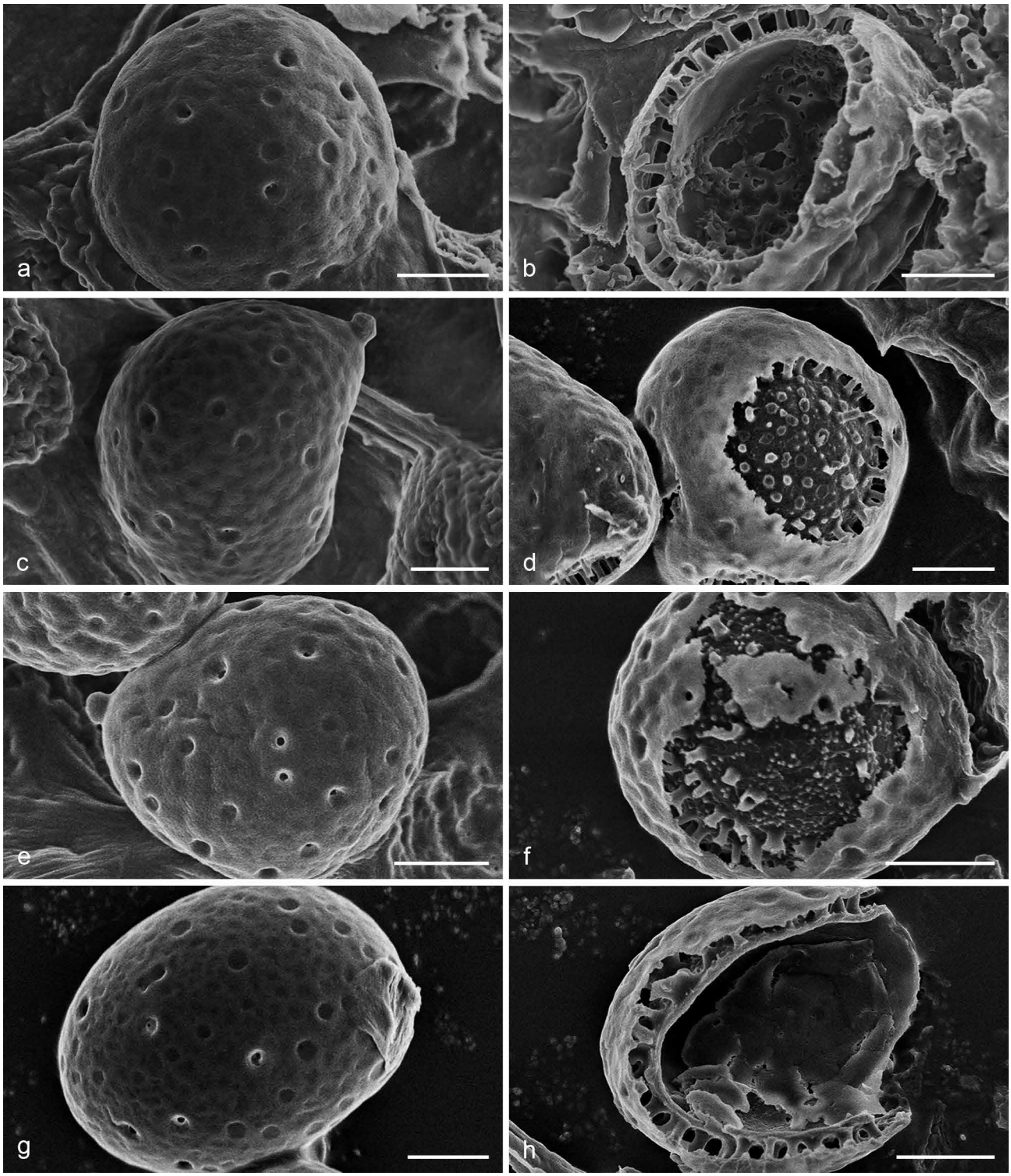

Fig. 3 Scanning Electron Micrograph (SEM) of basidiospores of *Foraminispora*. a–b. *Fo. austrosinensis* (Cui 16425); c–d. *Fo. concentrica* (Cui 12648); e–f. *Fo. yinggelingensis* (Cui 13618); g–h. *Fo. yunnanensis* (Cui 7974). a, c, e, g: General view showing exospore wall; b, d, f, h: detail in endospore ornamentation. — Scale bars: a–h = 2 µm.

brown when dry, dull, tomentose, with concentric furrows and radial wrinkles, sagging at the centre; margin acute to obtuse, entire, wavy and incurved when dry. Pore surface white to cream buff when fresh, colour unchanging when bruised, pale yellow when dry, even ferruginous in old specimens; pores circular to angular, 6–7 per mm; dissepiments slightly thick, entire. Context white to cream, without dark resinous lines, corky, up to 2 mm thick. Tubes concolorous with pore surface, hard corky, up to 3 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, swollen at base, up to 7.5 cm long and 1 cm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 2–4 µm diam; skeletal hyphae in context colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–3 µm diam; skeletal hyphae in tubes colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–5 µm diam; binding hyphae in tubes colourless, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate and inflated, often slanting to

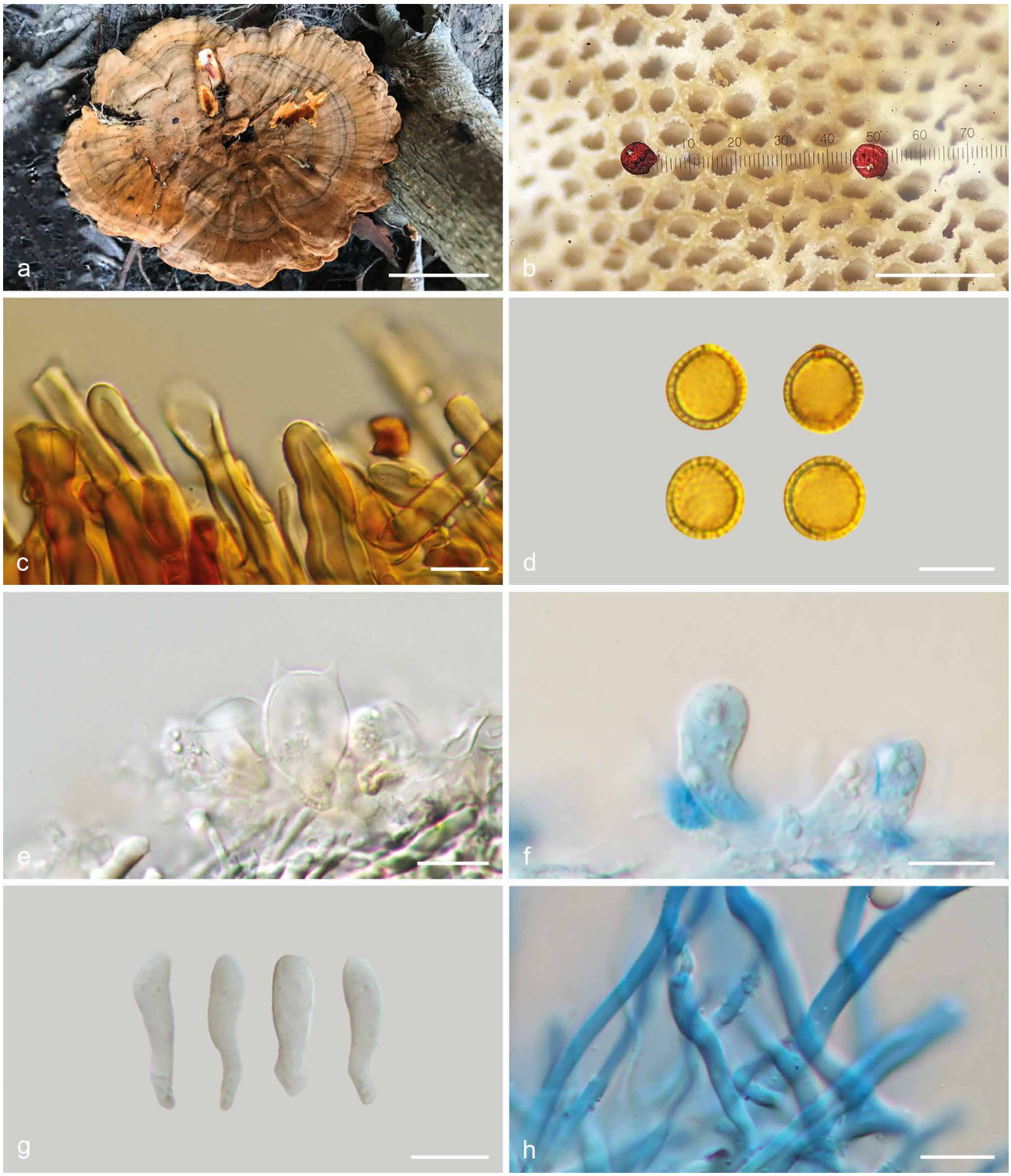

Fig. 4 Basidiomata and microscopic structures of *Foraminispora austrosinensis* (Cui 16425). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. cystidioles; h. skeletal hyphae from context. — Scale bars: a = 2.5 cm; b = 0.5 mm; c, e–h = 10 µm; d = 7 µm.

one side, yellowish brown, about 60–80 × 5–10 µm, forming a regular palisade. *Cystidia* absent; cystidioles clavate, colourless, thin-walled, 18–20 × 4–5 µm. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 13–23 × 11–14 µm; basidioles in shape similar to basidia, colourless, thin-walled, 13–17 × 6–10 µm. *Basidiospores* globose to subglobose, pale yellow, IKI–, CB+, with double and distinctly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (7–)7.2–8.5(–8.7) × (5.8–)6.7–8(–8.3) µm, L = 7.87 µm, W = 7.37 µm, Q = 1.06–1.07 (n = 60/2). Under SEM, exospore wall uneven or foveolate; endospore wall with some hollow and columnar spinules which persist to exospore wall forming holes.

Specimens examined. China, Hainan Province, Changjiang County, Yajia Forest Farm, on ground, 20 Apr. 1977, *S.J. Han*, HMAS 42695 (holotype, HMAS); Yunnan Province, Lincang County, 5 Aug. 2015, *B.K. Cui*, Cui 14318 (BJFC); ibid., Cui 14319 (BJFC). – Vietnam, Lam Dong Province, Bidoup-Nuiba National Park, 15 Oct. 2017, *B.K. Cui*, Cui 16425 (BJFC).

Notes — *Amauroderma austrosinense* was described from the tropical part of China (Zhao et al. 1984). It has the typical features such as white to straw colour pore surface when fresh and colour unchanging when bruised, cream context, hollow and columnar spinules on endospore wall which persist to the exospore wall forming the holes (Fig. 3a–b) that characterise *Foraminispora* (Costa-Rezende et al. 2017). In the phylogenetic

analyses, *A. austrosinense* was shown as a distinct lineage in *Foraminispora* with high support (100 % ML, 1.00 BPP). Therefore, we transferred *A. austrosinense* to *Foraminispora* as a new combination.

Foraminispora concentrica (J. Song, Xiao L. He & B.K. Cui) Y.F. Sun & B.K. Cui, *comb. nov.* — MycoBank MB828441; Fig. 3c–d, 5

Basionym. *Amauroderma concentricum* J. Song, Xiao L. He & B.K. Cui, Phytotaxa 260: 47. 2016.

Basidiomata annual, centrally to laterally stipitate, coriaceous to corky. Pileus single, orbicular to suborbicular, up to 11 cm diam and 1 cm thick. Pileal surface yellowish brown to reddish brown, dull, tomentose, with obvious concentric zones and radial wrinkles, slightly sagging at the centre; margin acute, entire, faintly wavy and incurved when dry. Pore surface white when fresh, colour unchanging when bruised, pale yellow to straw colour when dry; pores circular to angular, 3–5 per mm; dissepiments thin to slightly thick, entire. Context white to cream, without dark resinous lines, corky, up to 4 mm thick. Tubes concolorous with pore surface, hard corky, up to 6 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, slightly swollen at base, up to 7.5 cm long and 6 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context

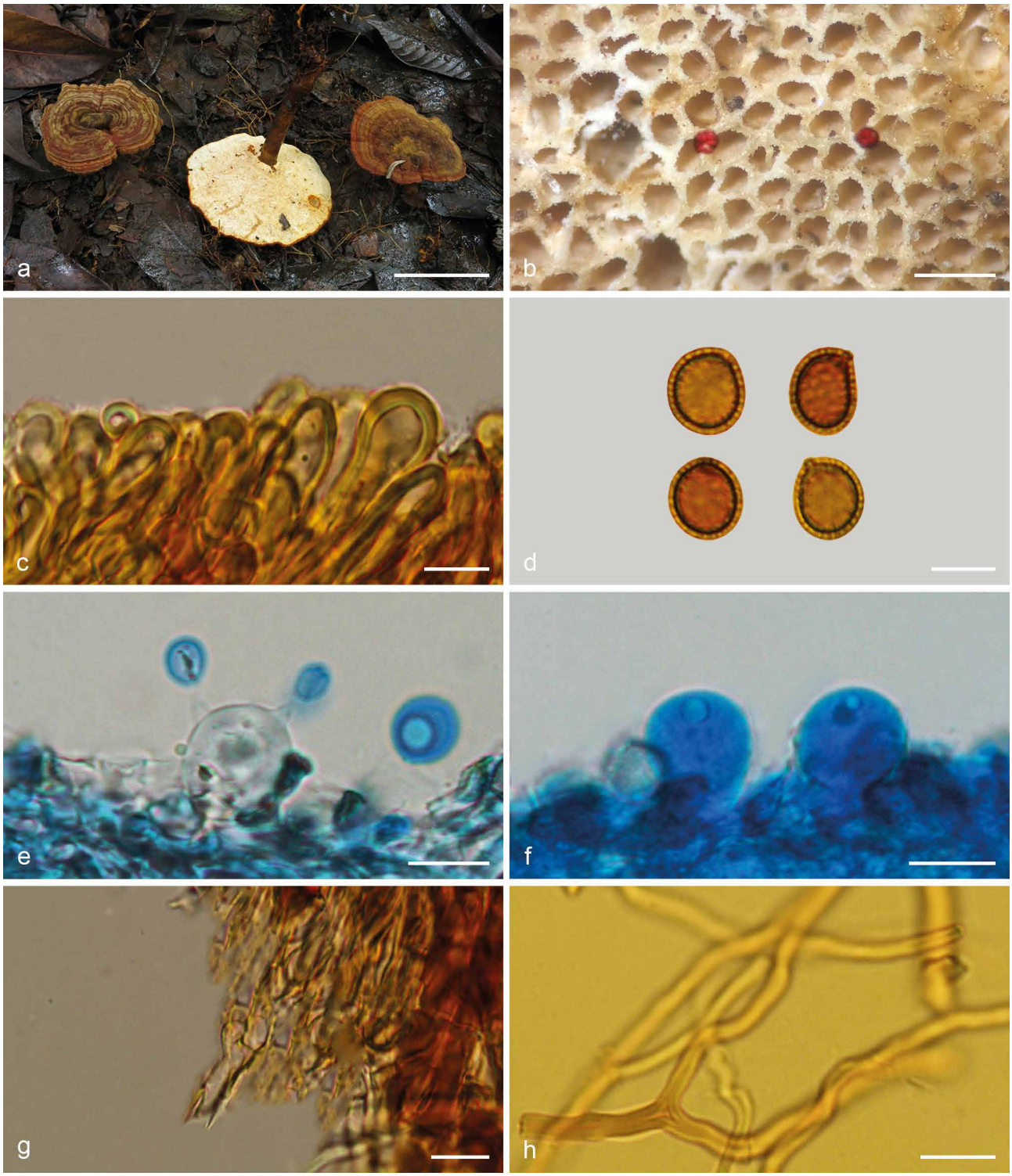

Fig. 5 Basidiomata and microscopic structures of *Foraminispora concentrica* (Cui 12648). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. generative hyphae from context; h. skeletal hyphae from context. — Scale bars: a = 3 cm; b = 0.5 mm; c, e–h = 10 µm; d = 7 µm.

colourless, thin-walled, 3–4 µm diam, often collapsed; skeletal hyphae in context colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–6 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–3 µm diam; skeletal hyphae in tubes pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–5 µm diam; binding hyphae in tubes colourless, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, inflated or constricted, faintly slanting to one side, yellowish brown, about 30–60 × 6–11 µm, forming a regular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 17–25 × 10–14 µm; basidioles in shape similar to basidia, colourless, thin-walled, 15–22 × 7–12 µm. *Basidiospores* subglobose to broadly ellipsoid, pale yellow, slightly dextrinoid, CB+, with double and distinctly thick walls, exospore wall smooth, endospore wall with conspicuous echinules, (6.8–)7.7–9.5(–9.6) × (6–)6.8–8.3(–9) µm, L = 8.6 µm, W = 7.48 µm, Q = 1.13–1.17 (n = 60/2). Under SEM, exospore wall uneven or foveolate, endospore wall with some hollow and columnar spinules which persist to exospore wall forming holes.

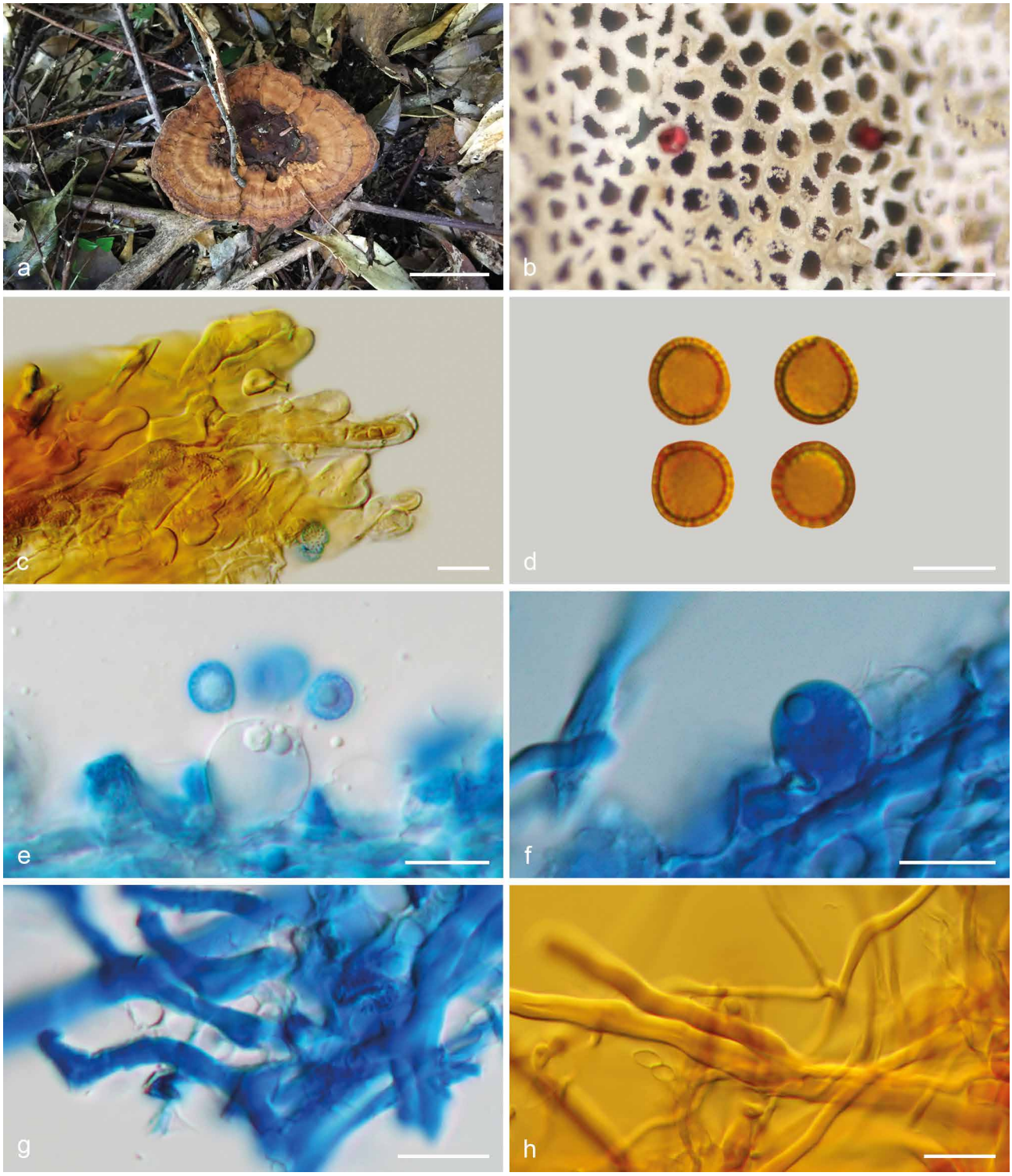

Fig. 6 Basidiomata and microscopic structures of *Foraminispora yinggelingensis* (Cui 13618). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. skeletal hyphae from tubes; h. skeletal and binding hyphae from context. — Scale bars: a = 2.5 cm; b = 0.5 mm; c, e–h = 10 µm; d = 7 µm.

Specimens examined. China, Sichuan Province, Mianning County, Lingshansi Park, on ground of angiosperm forest, 13 Sept. 2015, *B.K. Cui*, Cui 12644 (holotype, BJFC); ibid., Cui 12646 (paratype, BJFC); ibid., Cui 12647 (paratype, BJFC); ibid., Cui 12648 (paratype, BJFC); Yunnan Province, Lanping County, Luoguqing, 18 Sept. 2017, *B.K. Cui*, Cui 16238 (BJFC); ibid., *Cui* 16239 (BJFC); ibid., Cui 16240 (BJFC); Guizhou Province, Liupanshui, Lingshansi Park, on stump of angiosperm tree, 15 Oct. 2018, *H.J. Li*, Cui 1510 (BJFC).

Notes — *Amauroderma concentricum* is distributed in temperate and subtropical areas of China. Based on its typical features and phylogenetic support, we transfer *A. concentricum* to *Foraminispora* as a new combination. *Foraminispora concentrica* is similar to *Fo. austrosinensis* by the yellow brown and tomentose concentrically zonate pileal surface, white context and pore surface, but the pores (6–7 per mm) and basidiospores (7.2–8.5 × 6.7–8 µm) of *Fo. austrosinensis* are relatively smaller than *Fo. concentrica*; moreover, the basidiospores of *Fo. concentrica* are slightly dextrinoid, while *Fo. austrosinensis* has non-dextrinoid basidiospores.

Foraminispora yinggelingensis Y.F. Sun & B.K. Cui, *sp. nov*. — MycoBank MB828434; Fig. 3e–f, 6

Etymology. *Yinggelingensis* (Lat.), refers to Yinggeling, the type locality of this species.

Holotype. China, Hainan Province, Baisha County, Yinggeling Nature Reserve, on ground of angiosperm forest, 17 Nov. 2015, *B.K. Cui*, Cui 13618 (BJFC).

Diagnosis. *Foraminispora yinggelingensis* is characterized by its woody hard basidiomata, umbelliform pileus with obvious concentric dark zones, bright yellow generative hyphae in pileal cover, and slightly dextrinoid basidiospores.

Basidiomata annual, centrally stipitate, woody hard. Pileus single, suborbicular to umbelliform, up to 7 cm diam and 4 mm thick. Pileal surface yellowish brown to ferruginous when dry, dull, tomentose, with obvious concentric dark zones and radial wrinkles, slightly sagging at the centre; margin obtuse, entire, flat or incurved and wavy when dry, extending to pore surface. Pore surface white when fresh, colour unchanging when bruised, pale yellow when dry; pores subcircular to angular or irregular, 5–7 per mm; dissepiments slightly thick, entire. Context pale buff, without dark resinous lines, hard corky, up to 2 mm thick. Tubes straw colour, woody hard, up to 2 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, up to 6 cm long and 6 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 2–3 µm diam; skeletal hyphae in context colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–5 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, up to 3 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–3 µm diam; skeletal hyphae in tubes colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–4 µm diam; binding hyphae in tubes colourless, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, faintly slanting to one side and tortuous, bright yellow, about 50–80 × 5–12 µm, forming an irregular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 16–21 × 11–13 µm; basidioles in shape similar to basidia, colourless, thin-walled, 11–15 × 5–11 µm. *Basidiospores* globose to subglobose, pale yellow, slightly dextrinoid, CB+, with double and distinctly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (7–)7.2–8.5(–8.7) × 6.6–8 µm, L = 7.89 µm, W = 7.17 µm, Q = 1.1 (n = 60/1). Under SEM, exospore wall uneven or foveolate, endospore wall with some hollow and columnar spinules which persist to exospore wall forming holes.

Additional specimen (paratype) examined. China, Hainan Province, Baisha County, Yinggeling Nature Reserve, on ground of angiosperm forest, 17 Nov. 2015, *B.K. Cui*, Cui 13630 (BJFC).

Notes — *Foraminispora yinggelingensis* was collected from the tropical part of China. It is similar to *Fo. austrosinensis* in the umbelliform basidiomata, white to cream context and pore surface, and similar basidiospores, but the woody hard basidiomata, the absence of cystidioles and the slightly dextrinoid basidiospores of *Fo. yinggelingensis* make it different from *Fo. austrosinensis*. In phylogenetic analyses, these two species nested in two well-supported lineages (Fig. 1, 2).

Foraminispora yunnanensis (J.D. Zhao & X.Q. Zhang) Y.F. Sun & B.K. Cui, *comb. nov*. — MycoBank MB828442; Fig. 3g–h, 7

Basionym. *Amauroderma yunnanense* J.D. Zhao & X.Q. Zhang, Acta Mycol. Sin. S1: 268. 1986.

Basidiomata annual, centrally to laterally stipitate, coriaceous to corky. Pileus single, suborbicular to flabelliform, up to 6.5 cm diam and 6 mm thick. Pileal surface cinnamon to reddish brown when dry, dull, tomentose, with faintly concentric furrows at the margin and irregular wrinkles; margin subacute to obtuse, entire and wavy when dry. Pore surface white to pale straw, colour unchanging when bruised; pores circular to angular, 2–3 per mm; dissepiments thin, fragile when dry. Context white to pale yellow, without dark resinous lines, corky, up to 2 mm thick. Tubes concolorous with pore surface, occasionally fascicular, woody hard, up to 4 mm long. Stipe concolorous with pileal surface, cylindrical and solid, slightly swollen at base, up to 8 cm long and 6 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 3–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, 1–3 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–4 µm diam; skeletal hyphae in tubes colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–5 µm diam; binding hyphae in tubes colourless, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, inflated or constricted, arranged loosely, yellowish brown, about 40–60 × 6–9 µm, forming an irregular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 20–35 × 11–18 µm; basidioles in shape similar to basidia, colourless, thin-walled, 13–23 × 6–10 µm. *Basidiospores* broadly ellipsoid to ellipsoid, pale yellow, IKI–, CB+, with double and distinctly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, 8–10.7(–11.2) × (6.8–)7–8.3(–8.7) µm, L = 9.35 µm, W = 7.63 µm, Q = 1.18–1.27 (n = 60/2). Under SEM, exospore wall uneven or foveolate, endospore wall with some hollow and columnar spinules which persist to exospore wall forming holes.

Specimens examined. China, Yunnan Province, Xichou County, Xiaoqiaogou, on ground, 14 May 1959, *Q.Z. Wang*, HMAS 48231 (holotype, HMAS); Kunming, Qiongzhusi Park, on ground of angiosperm forest, 21 Oct. 2009, *B.K. Cui*, Cui 7974 (BJFC).

Notes — *Foraminispora yunnanensis* can be distinguished by large lacerate pores (2–3 per mm), occasionally fascicular tubes and broadly ellipsoid to ellipsoid basidiospores. It is also consistent with *Foraminispora* in the unique ultrastructural

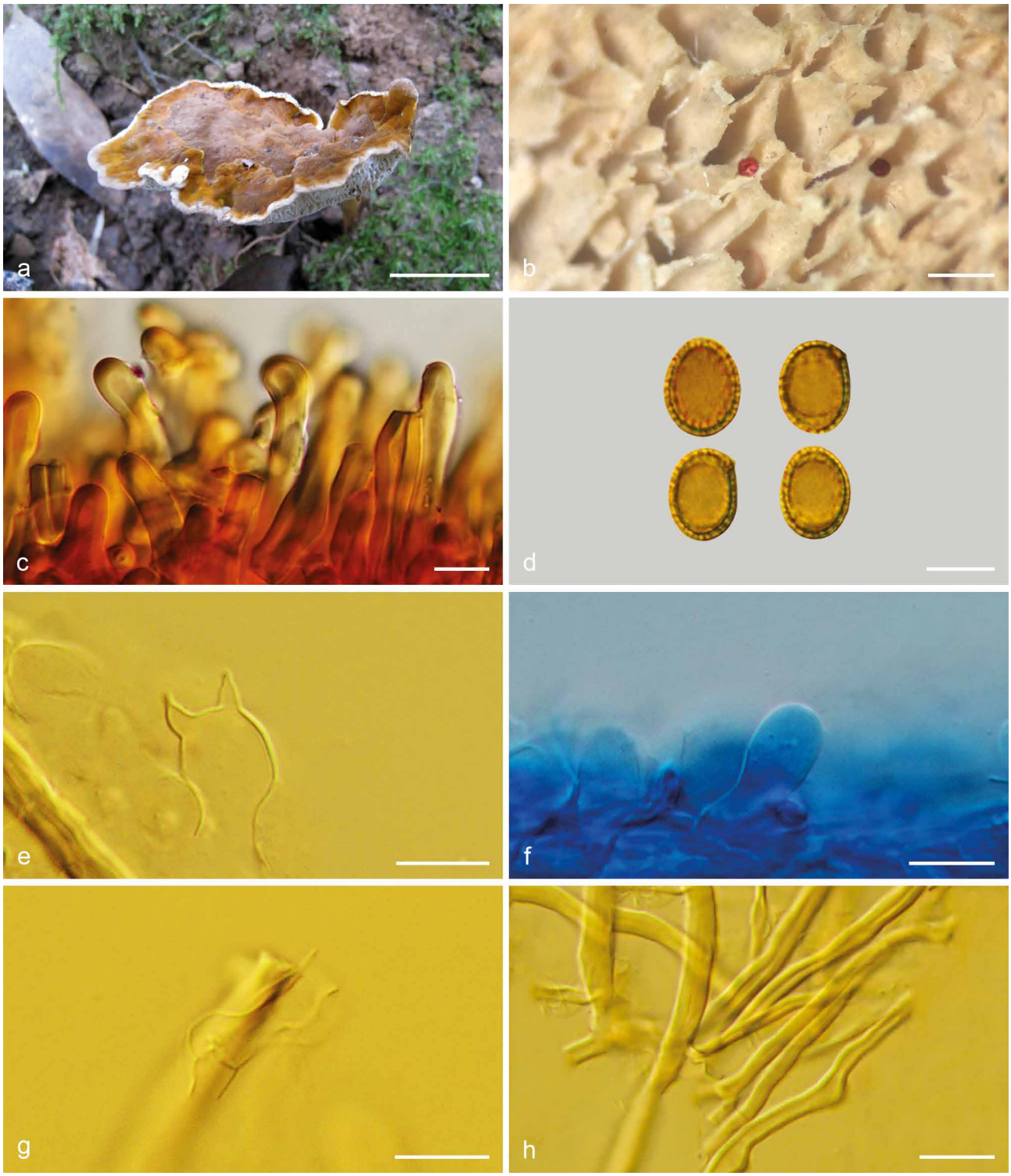

Fig. 7 Basidiomata and microscopic structures of *Foraminispora yunnanensis* (Cui 7974). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. generative hyphae from context; h. skeletal hyphae from tubes. — Scale bars: a = 2 cm; b = 0.5 mm; c, e–h = 10 µm; d = 7 µm.

characteristics of the exospore wall with obvious holes caused by hollow and columnar spinules on the endospore wall which persist to the exospore wall (Fig. 3g–h). In the phylogenetic analyses, *Fo. yunnanensis* was shown to be a distinct lineage in *Foraminispora* with high support (100 % ML, 1.00 BPP).

Furtadoa D.H. Costa, Robledo & Drechsler-Santos, Persoonia 39: 263. 2017 — MycoBank MB819014

Type species. *Furtadoa biseptata* D.H. Costa, Drechsler-Santos & Reck, Persoonia 39: 265. 2017.

Basidiomata annual, centrally to laterally stipitate, soft to corky. Pileus single, orbicular to flabelliform or infundibuliform. Pileal surface yellowish brown to greyish brown, dull, glabrous to tomentose, obviously concentrically zonate. Pore surface white to straw colour when dry; pores circular to angular; dissepiments thin to thick, entire to lacerate. Context yellow brown, with dark resinous lines, soft corky. Hyphae system monomitic to dimitic; context composed of clamped to simple-septate generative hyphae, thin- to slightly thick-walled; tubes composed of clamped generative hyphae and arboriform skeletal hyphae. Basidiospores subglobose to ellipsoid, colourless, double-walled with conspicuous endospore spinules, IKI–.

Notes — *Furtadoa* was established by Costa-Rezende et al. (2017) and all species (including *Fu. biseptata*, *Fu. brasiliensis*,

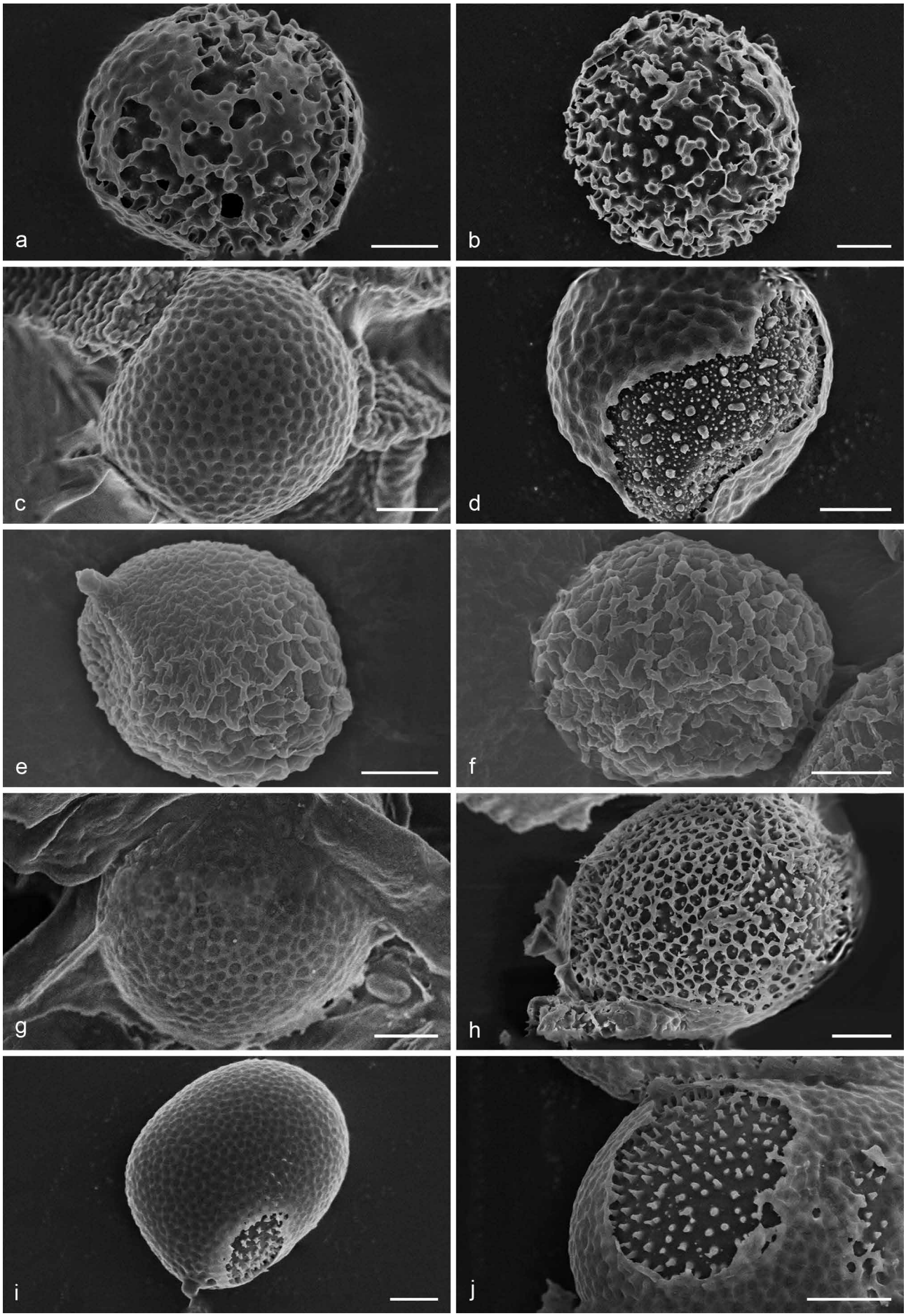

Fig. 8 Scanning Electron Micrograph (SEM) of basidiospores of *Sanguinoderma*. a–b. *S. bataanense* (Dai 10746); c–d. *S. elmerianum* (HMAS 133187); e–f. *S. flavovirens* (Cui 16935); g–h. *S. laceratum* (Cui 8155); i–j. *S. microporum* (Cui 13851); k–l. *S. perplexum* (Dai 10811); m–n. *S. reniforme* (Cui 16511); o–p. *S. rude* (MEL 2150776); q–r. *S. rugosum* (Cui 16377); s–t. *S. sinuosum* (MEL 2366586). a, c, e, g, i, k, m, o, q, s: General view showing exospore wall; b, d, f, h, j, l, n, p, r, t: detail in endospore ornamentation. — Scale bars: a–t = 2 µm.

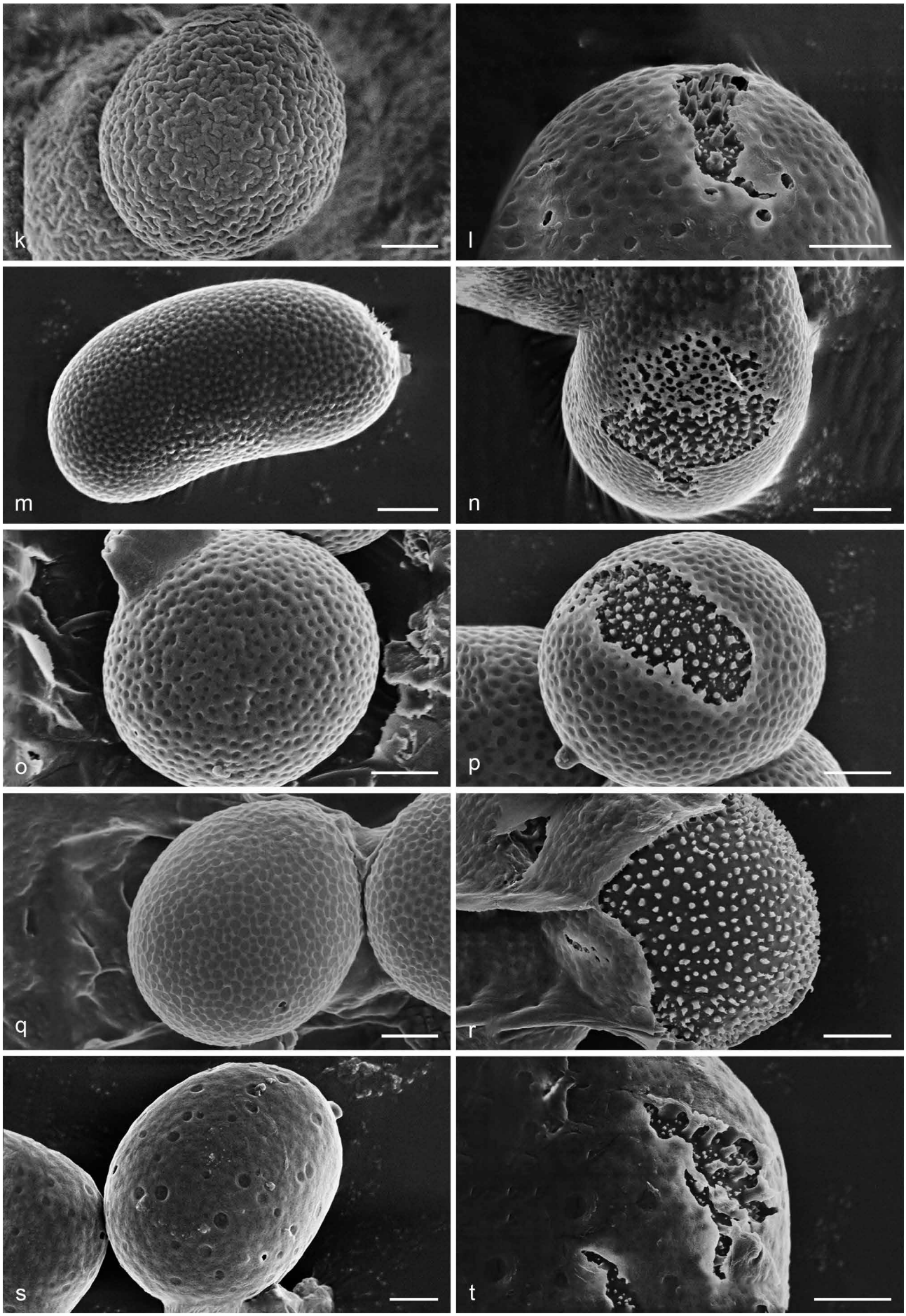

Fig. 8 (cont.)

Fu. corneri) have so far been found in the Neotropics. The genus is distinguished from the other genera in *Amauroderma* s.lat. by presenting a monomitic context. Based on the 4-gene and 6-gene phylogenetic analyses (Fig. 1, 2), we confirm the status of *Fu. biseptata* and *Fu. brasiliensis*. However, Gomes-Silva et al. (2015) considered that *Amauroderma corneri* was the synonymy of *A. brasiliense* according to the morphological features of funnel- to fan-shaped, soft basidiomata almost whitish when fresh, large pores (1–2 per mm) and non-dextrinoid basidiospores (8–10 × 7–9 µm). Therefore, we treated *Fu. corneri* as a synonymy of *Fu. brasiliensis* until molecular evidence is provided.

Key to accepted species of Furtadoa

1. Generative hyphae in context with both clamps and simple septa . . . . . *Fu. biseptata*
1. Generative hyphae in context with clamps only . . . . . *Fu. brasiliensis*

Sanguinoderma Y.F. Sun, D.H. Costa & B.K. Cui, *gen. nov.* — MycoBank MB828433

Etymology. *Sanguinoderma* (Lat.), refers to the genus producing *Amauroderma*-like basidiomata but with a fresh pore surface that changes to blood red when bruised.

Type species. *Sanguinoderma rude* (Berk.) Y.F. Sun, D.H. Costa & B.K. Cui.

Diagnosis. *Sanguinoderma* is characterized by basidiomata corky to woody hard, pileus dark, pore surface colour changing to blood red when bruised, basidiospores double-walled in which exospore wall semi-reticulate or vermiculate to verrucose, endospore wall with solid and columnar to coniform spinules under SEM.

Basidiomata annual, central or lateral stipitate to almost sessile, corky to woody hard. Pileus single, suborbicular to flatly reniform. Pileal surface dark brown to nearly black, dull, glabrous to tomentose, concentrically zonate or furrowed and radially rugose. Pore surface greyish white to dark grey when fresh, colour changing to blood red when bruised, then quickly darkening; pores circular to angular or irregular; dissepiments thin to thick, entire. Context pale brown to dark brown, with resinous lines, hard corky. Hyphal system trimitic; all hyphae IKI–, CB+; tissues darkening in KOH; generative hyphae colourless, thin-walled, with clamp connections; skeletal hyphae colourless to yellowish brown, thick-walled, arboriform branched and flexuous; binding hyphae colourless to pale yellow, subsolid, branched and flexuous. Basidiospores subglobose or ellipsoid to reniform, pale yellow, double and slightly to distinctly thick-walled, exospore wall semi-reticulate or vermiculate to verrucose, endospore wall with solid and columnar to coniform spinules under SEM, IKI–, CB+.

Notes — All examined specimens in *Sanguinoderma* were found in the Paleotropics and in Oceania. In the 4-gene and 6-gene based phylogenetic analyses (Fig. 1, 2) these species nested in eleven highly supported lineages. *Sanguinoderma* presents similar macro- and micro-morphology to *Amauroderma* s.str.; however, it can be distinguished by its conspicuous reaction in the pore surface, which rapidly changes to blood red when bruised. With the addition of morphological evidence, five new species are described and five new combinations are proposed and re-described. One taxon with insufficient morphological characters to separate it from other taxa is treated as *Sanguinoderma* sp.

Key to accepted species of Sanguinoderma

1. Pores ≤ 4 per mm 2
1. Pores > 4 per mm 5
2. Pore dissepiments lacerate, tubes fascicular when dry . . . . . *S. laceratum*
2. Pore dissepiments entire, tubes unchanged when dry . . 3
3. Basidiospores globose to subglobose, exospore wall verrucose with long and columnar endospore spinules . . . . . *S. bataanense*
3. Basidiospores subglobose to ellipsoid, exospore wall semi-reticulate to vermiculate with short to long and columnar to coniform endospore spinules 4
4. Basidiospores subglobose to broadly ellipsoid, medially thick-walled, exospore wall semi-reticulate with small and deep pits . . . . . *S. rude*
4. Basidiospores ellipsoid, distinctly thick-walled, exospore wall uneven with distinctly circular hollows . . . . . *S. sinuosum*
5. Pores surface yellowish green; basidiospores 8–9.2 × 6.4–7.2 µm . . . . . *S. flavovirens*
5. Pores surface pale white to dark grey; basidiospores 9–14 × 8–12 µm 6
6. Basidiomata almost sessile or with a very short and thick stipe . . . . . *S. perplexum*
6. Basidiomata with distinct stipe 7
7. Basidiomata laterally stipitate, pileus flatly reniform . . . . . *S. elmerianum*
7. Basidiomata centrally or laterally stipitate, pileus suborbicular to flabelliform 8
8. Pileal cover derived from loose generative hyphae; basidiospores reniform . . . . . *S. reniforme*
8. Pileal cover derived from compact generative hyphae; basidiospores subglobose to broadly ellipsoid 9
9. Pores 6–7 per mm with extremely thick dissepiments, yellowish brown . . . . . *S. microporum*
9. Pores 5–7 per mm with slightly thick dissepiments, greyish white to dark grey . . . . . *S. rugosum*

Sanguinoderma bataanense (Murrill) Y.F. Sun & B.K. Cui, *comb. nov.* — MycoBank MB828443; Fig. 8a–b, 9

Basionym. *Amauroderma bataanense* Murrill, Bull. Torrey Bot. Club 35: 407. 1908.

≡ *Ganoderma bataanense* (Murrill) Sacc. & Trotter, Syll. Fung. 21: 307. 1912.

≡ *Polystictus bataanensis* (Murrill) Sacc. & Trotter, Syll. Fung. 21: 322. 1912.

Basidiomata annual, laterally stipitate, soft to hard corky. Pileus single, suborbicular to flabelliform, up to 3.5 cm diam and 8 mm thick. Pileal surface dark yellowish brown when dry, dull, glabrous, with concentric furrows and radial wrinkles; margin obtuse, entire, wavy and incurved when dry. Pore surface greyish white when fresh, colour changing to blood red when bruised, then quickly darkening; pores subcircular to irregular, 1–4 per mm; dissepiments thin, entire. Context dark brown, with thick black stratum, corky, up to 2 mm thick. Tubes darker than context, woody hard, up to 6 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, slightly swollen at the base, up to 4.5 cm long and 3 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 2–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–6 µm diam; binding hyphae in context pale yellow, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colour-

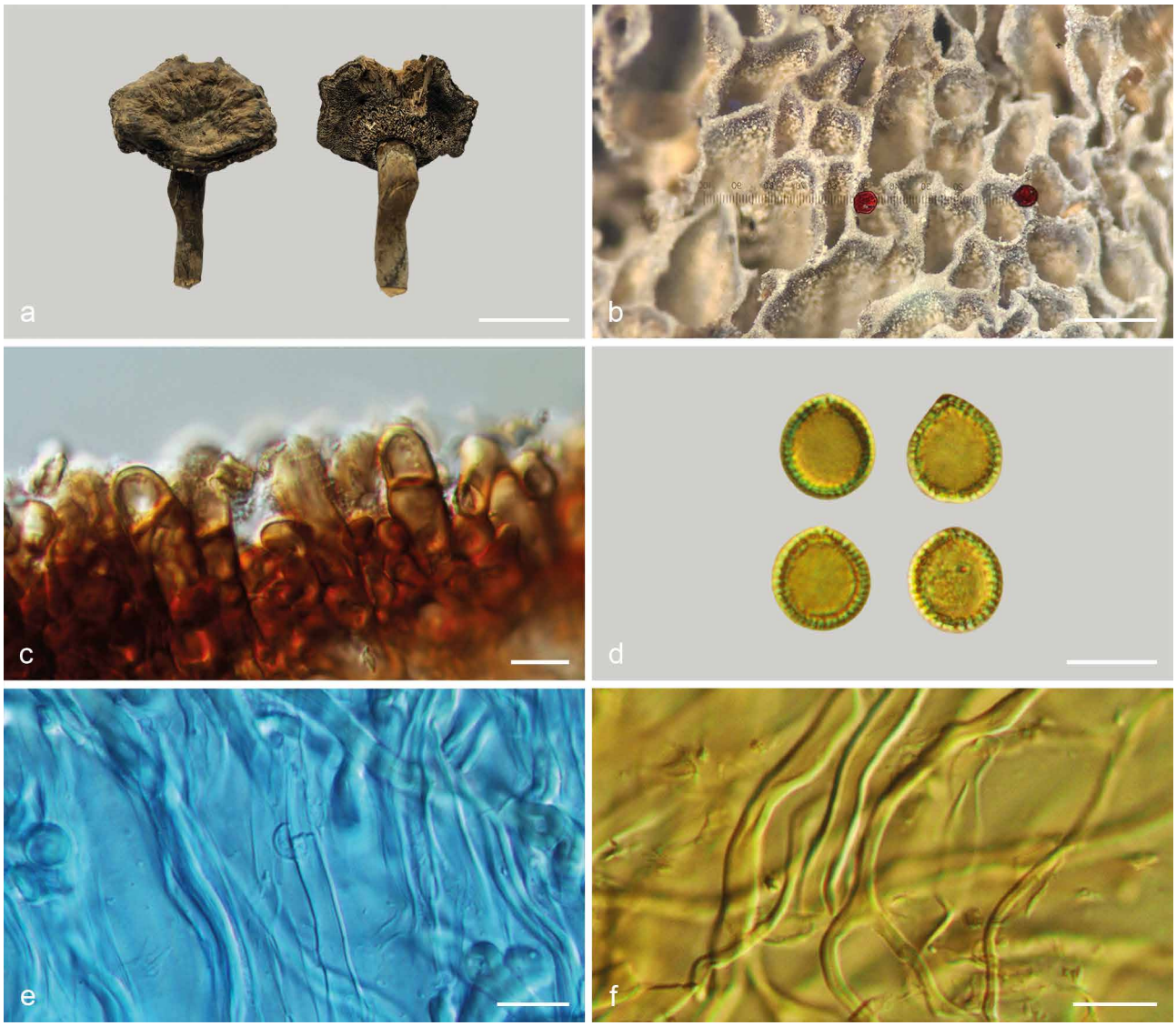

Fig. 9 Basidiomata and microscopic structures of *Sanguinoderma bataanense* (Dai 10746). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. generative hyphae from tubes; f. skeletal hyphae from context. — Scale bars: a = 2 cm; b = 0.5 mm; c–f = 10 µm.

less, thin-walled, 2–3 µm diam; skeletal hyphae in tubes pale yellow, thick-walled with a wide or narrow lumen to subsolid, arboriform branched and flexuous, up to 7 µm diam; binding hyphae in tubes pale yellow, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate with obvious septa, slightly inflated, reddish brown, about 30–70 × 5–9 µm, forming a regular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 30–40 × 12–16 µm; basidioles in shape similar to basidia, colourless, thin-walled, 25–30 × 8–13 µm. *Basidiospores* globose to subglobose, pale yellow, IKI–, CB+, with double and distinctly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (9.6–)10–12.5(–13.1) × (8.5–)9–11(–11.3) µm, L = 11.13 µm, W = 9.84 µm, Q = 1.13 (n = 60/2). Under SEM, exospore wall thin and badly worn, endospore wall with long and thick columnar spinules which are loosely arranged and cause conspicuous warts on exospore wall (Fig. 8a–b).

Specimens examined. China, Hainan Province, Danzhou, on stump of *Litchi chinensis*, 7 May 2009, *B.K. Cui*, Cui 6285 (BJFC); ibid., *Y.C. Dai*, Dai 10746 (BJFC); Guangxi Autonomous Region, Baise, Jinzhongshan Nature Reserve, on rotten wood, 21 Oct. 1957, *L.W. Xu*, HMAS 23492 (HMAS).

Notes — *Amauroderma bataanense* was described from the Philippines (Murrill 1908). We collected it from the tropical areas of China. It can be distinguished by its fresh pore surface colour that changes to blood red when bruised, subcircular to irregular pores (1–4 per mm) with thin and entire dissepiments, and distinctly thick-walled basidiospores. In the phylogenetic analyses, *A. bataanense* was shown to be a distinct well-supported lineage in *Sanguinoderma* with strong support (Fig. 1, 2). Therefore, we transferred *A. bataanense* to *Sanguinoderma*.

Sanguinoderma elmerianum (Murrill) Y.F. Sun & B.K. Cui, *comb. nov*. — MycoBank MB828444; Fig. 8c–d, 10

Basionym. *Amauroderma elmerianum* Murrill, Bull. Torrey Bot. Club 34: 475. 1907.

≡ *Ganoderma elmerianum* (Murrill) Sacc. & Trotter, Syll. Fung. 21: 305. 1912.

Basidiomata annual, lateral stipitate to almost sessile, coriaceous to soft corky. Pileus single, flatly reniform, up to 14.5 cm diam and 1 cm thick. Pileal surface dark brown to nearly black, dull, glabrous, with concentric furrows and radial wrinkles; margin obtuse, entire, slightly wavy and flat when dry. Pore surface pale brown to pale grey when fresh, colour changing to blood red when bruised, then quickly darkening; pores circular to angular, 5–7 per mm; dissepiments slightly thick, entire. Context pale brown to cinnamon, with two dark melanoid lines, soft corky, up to 4 mm thick. Tubes slightly darker than

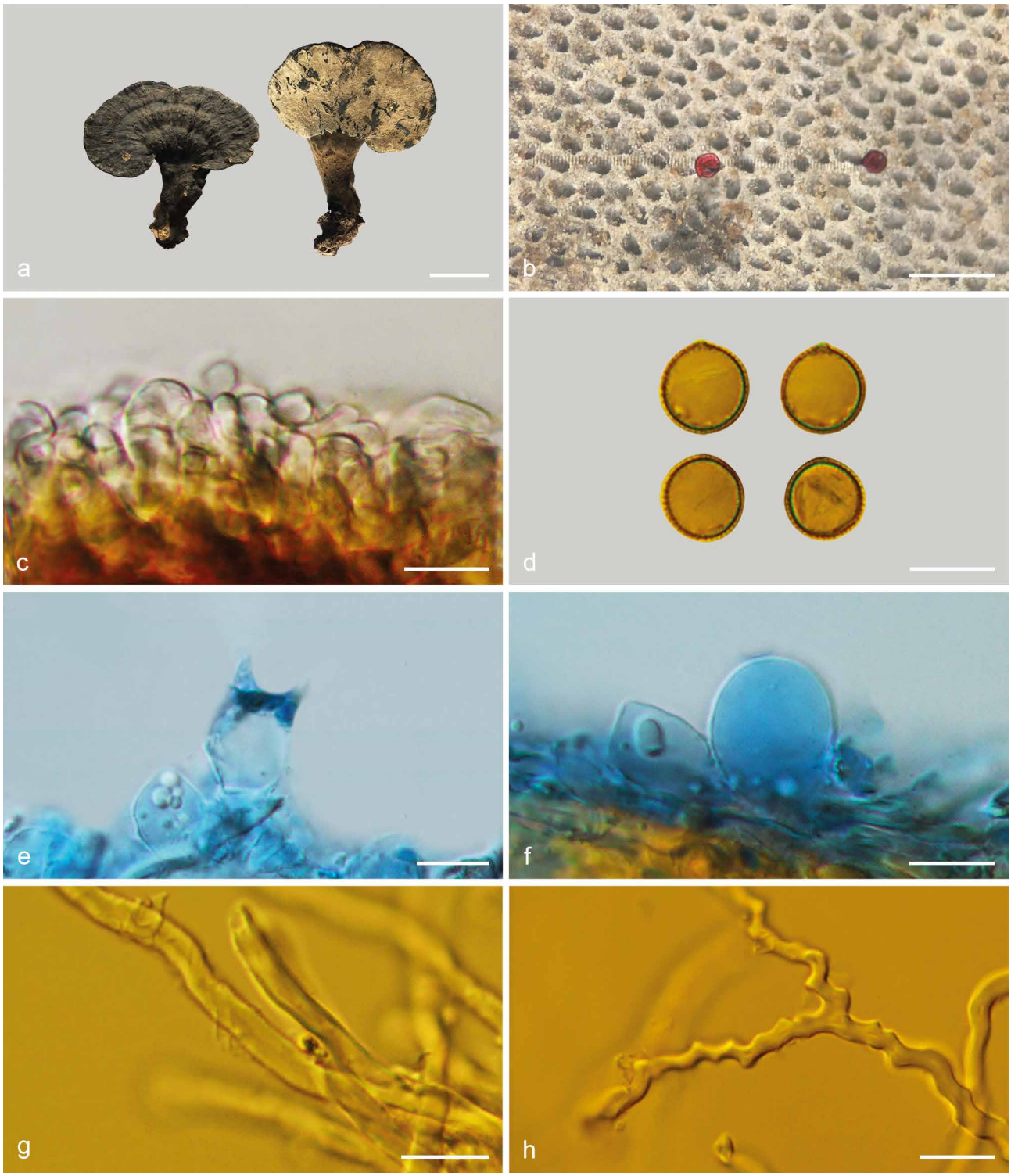

Fig. 10 Basidiomata and microscopic structures of *Sanguinoderma elmerianum* (HMAS 133187). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. skeletal hyphae from tubes; h. binding hyphae from context. — Scale bars: a = 5 cm; b = 0.5 mm; c–h = 10 µm.

context, concolorous with pore surface, hard corky, up to 6 mm long. Stipe concolorous with pileal surface, cylindrical, swollen at base, about 9 cm long and 3 cm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, binding hyphae usually serrated, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 2–4 µm diam, usually collapsed; skeletal hyphae in context colourless to pale yellow, thick-walled with a wide or narrow lumen to subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–4 µm diam; skeletal hyphae in tubes pale yellow, with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–7 µm diam; binding hyphae in tubes colourless to pale yellow, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate with obvious septa, inflated and slightly tortuous, pale brown to reddish brown, about 30–50 × 5–9 µm, forming a regular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, about 22–25 × 10–17 µm; basidioles in shape similar to basidia, colourless, thin-walled, 14–22 × 6–13 µm. *Basidiospores* globose to subglobose, pale yellow, IKI–, CB+, with double and medially thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (8.4–)9.2–11.1(–11.2) × (7.8–)9–10.1(–10.5) µm, L = 10.26

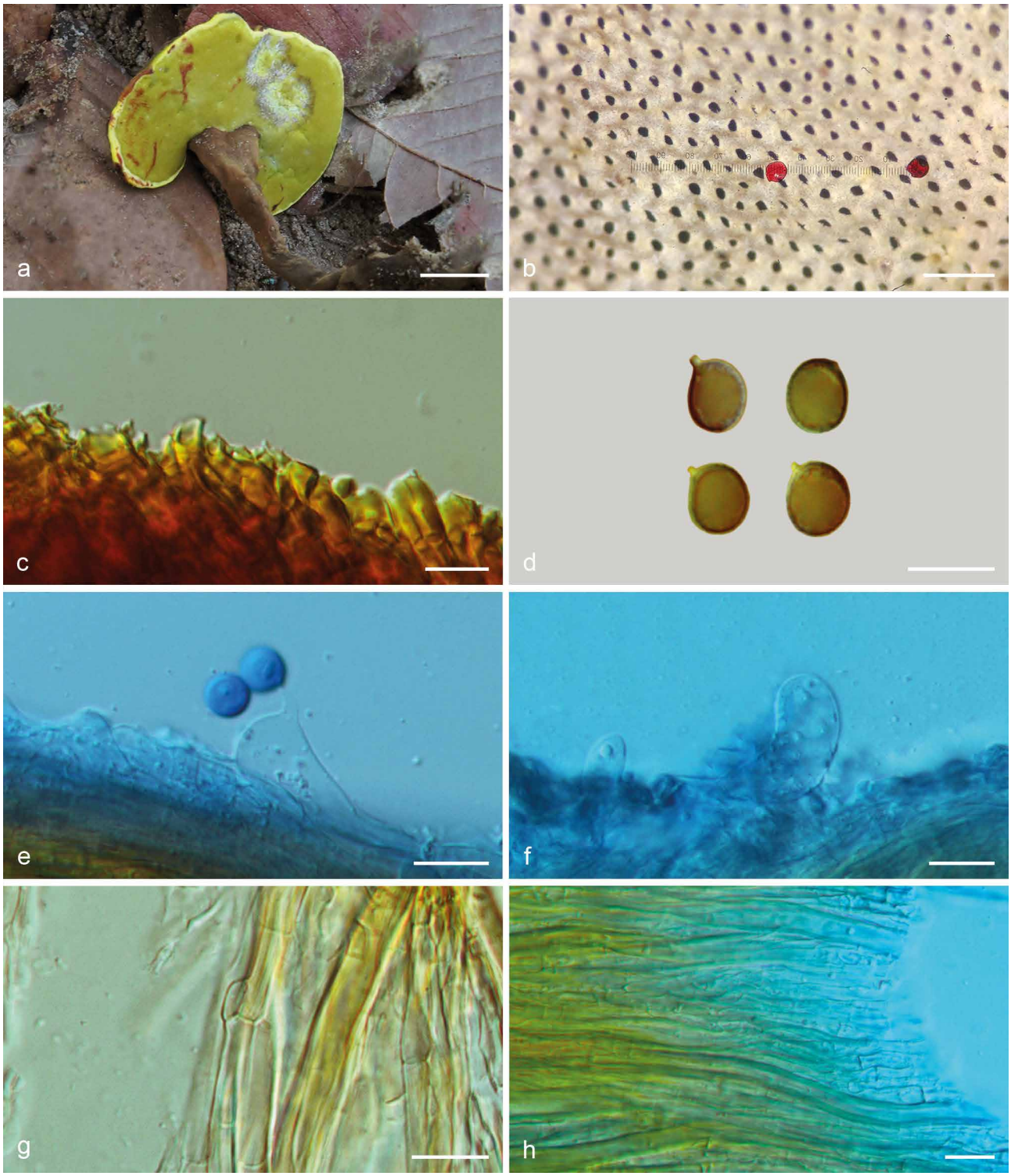

Fig. 11 Basidiomata and microscopic structures of *Sanguinoderma flavovirens* (Cui 16935). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. generative hyphae from tubes; h. regularly arranged hyphae from context. — Scale bars: a = 1 cm; b = 0.5 mm; c–h = 10 µm.

µm, W = 9.5 µm, Q = 1.07–1.09 (n = 60/2). Under SEM, exospore wall alveolate to semi-reticulate, endospore wall with long and medially thick coniform spinules loosely arranged.

Specimens examined. China, Yunnan Province, Xishuangbanna, Baka Xiao Zhai Nature Reserve, 5 Aug. 2003, *T.Z. Wei*, HMAS 133187 (HMAS); Guangdong Province, Zhaoqing, Dinghushan Nature Reserve, dead angiosperm tree, 30 June 2010, *B.K. Cui*, Cui 8940 (BJFC).

Notes — *Amauroderma elmerianum* was described from the Philippines (Murrill 1907). The specimens collected from China have soft basidiomata with a flat reniform pileus, and globose to subglobose basidiospores with an ornamented endospore wall (Fig. 8c–d); characters which are consistent with the previous descriptions (Murrill 1907, Furtado 1981). In the phylogenetic analyses, *A. elmerianum* was shown as a distinct well-supported lineage in *Sanguinoderma* with high support (100 % ML, 1.00 BPP). Therefore, we transferred *A. elmerarium* to *Sanguinoderma*.

Sanguinoderma flavovirens Y.F. Sun & B.K. Cui, *sp. nov.* — MycoBank MB828435; Fig. 8e–f, 11

Etymology. *Flavovirens* (Lat.), refers to the yellowish green pore surface when fresh.

Holotype. Zambia, Ndola, Ngosa Village, on ground of angiosperm forest, 5 Jan. 2018, *Bo Zhang*, Cui 16935 (BJFC; isotype IFP).

Diagnosis. *Sanguinoderma flavovirens* differs from other species in this genus by its yellowish green pore surface with distinctly thick dissepiments, almost regularly arranged hyphae in context, and relatively small basidiospores.

Basidiomata annual, laterally stipitate, hard corky. Pileus single, suborbicular, up to 4.5 cm diam and 5 mm thick. Pileal surface dark yellowish brown when dry, dull, glabrous, with obvious concentric furrows and faint radial wrinkles; margin obtuse, entire, wavy and incurved when dry. Pore surface yellowish green when fresh, colour changing to blood red when bruised, then quickly darkening; pores circular to angular, 5–6 per mm; dissepiments distinctly thick, entire. Context straw colour, with dark melanoid lines, corky, up to 2 mm thick. Tubes nearly black when dry, hard corky, up to 3 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, tapering at the base, up to 6 cm long and 7 mm diam. *Hyphal system* trimitic; hyphae almost regularly arranged in context, generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 3–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen, slightly flexuous, 3–7 µm diam; binding hyphae in context colourless, subsolid, rarely branched and slightly flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, 2–4 µm diam; skeletal hyphae in tubes pale yellow to bright yellow, thick-walled with a wide to narrow lumen, slightly flexuous, up to 7 µm diam; binding hyphae in tubes pale yellow, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, faintly slanting to one side and flexuous, yellowish brown to reddish brown, about 30–50 × 4–7 µm, forming a regular palisade. *Cystidia* or *cystidioles* absent. *Basidia* clavate, colourless, thin-walled, 18–27 × 9–18 µm; basidioles in shape similar to basidia, colourless, thin-walled, 15–20 × 5–11 µm. *Basidiospores* subglobose to broadly ellipsoid, pale yellow, IKI–, CB+, with double and slightly thick walls, exospore wall smooth, endospore wall with indistinct spinules, 8–9.2(–9.3) × (6–)6.4–7.2 µm, L = 8.61 µm, W = 6.85 µm, Q = 1.26 (n = 60/1). Under SEM, exospore wall reticulate to vermiculate with obvious warts.

Notes — *Sanguinoderma flavovirens* was collected from Zambia. It is a distinct species on account of the yellowish green pore surface when fresh, colour changing to blood red when bruised, which is the typical feature of *Sanguinoderma*. In addition, *S. flavovirens* was shown to be a distinct lineage in *Sanguinoderma* through 4-gene and 6-gene phylogenetic analyses (Fig. 1, 2).

Sanguinoderma laceratum Y.F. Sun & B.K. Cui, *sp. nov*. — MycoBank MB828436; Fig. 8g–h, 12

Etymology. *Laceratum* (Lat.), refers to the lacerate pores.

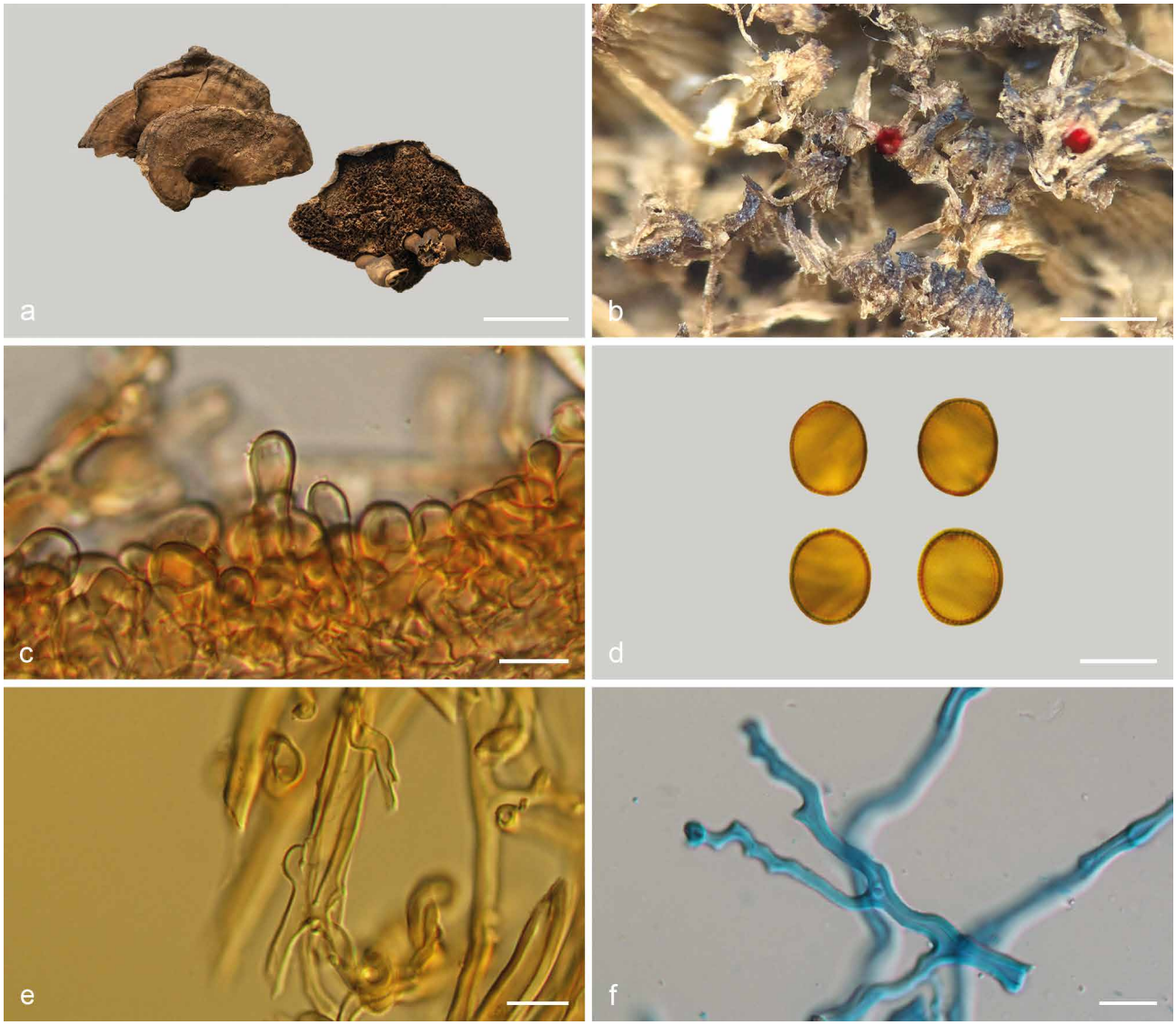

Fig. 12 Basidiomata and microscopic structures of *Sanguinoderma laceratum* (Cui 8155). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. generative hyphae from tubes; f. skeletal hyphae from context. — Scale bars: a = 3.5 cm; b = 1.5 mm; c–f = 10 µm.

Holotype. China, Yunnan Province, Baoshan, Gaoligongshan Nature Reserve, on fallen angiosperm trunk, 25 Sept. 2009, *B.K. Cui*, Cui 8155 (BJFC; isotype IFP).

Diagnosis. *Sanguinoderma laceratum* differs from other species in this genus by a combination of soft basidiomata with superposed pileus, lacerate pores with thin dissepiments, and tubes becoming fascicular when dry.

Basidiomata annual, laterally stipitate, soft corky. Pileus multiple and superposed, flabelliform or reniform, up to 7.5 cm diam and 1 cm thick. Pileal surface dark cinnamon when dry, dull, tomentose, with faint concentric zones and radial wrinkles; margin acute, entire, wavy and incurved when dry. Pore surface pale buff to greyish brown when fresh, colour changing to blood red when bruised, becoming dark brown to nearly black; pores irregular, 2–3 per mm; dissepiments thin, lacerate when dry. Context straw colour to pale brown, with pale grey melanoid lines, soft corky, up to 4 mm thick. Tubes concolorous with context, woody hard, becoming fascicular when dry, up to 6 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, up to 8.5 cm long and 4 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, slightly thick-walled, 3–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–7 µm diam; binding hyphae in context pale yellow, subsolid, branched and flexuous, up to 2 µm diam. Generative hyphae in tubes colour-

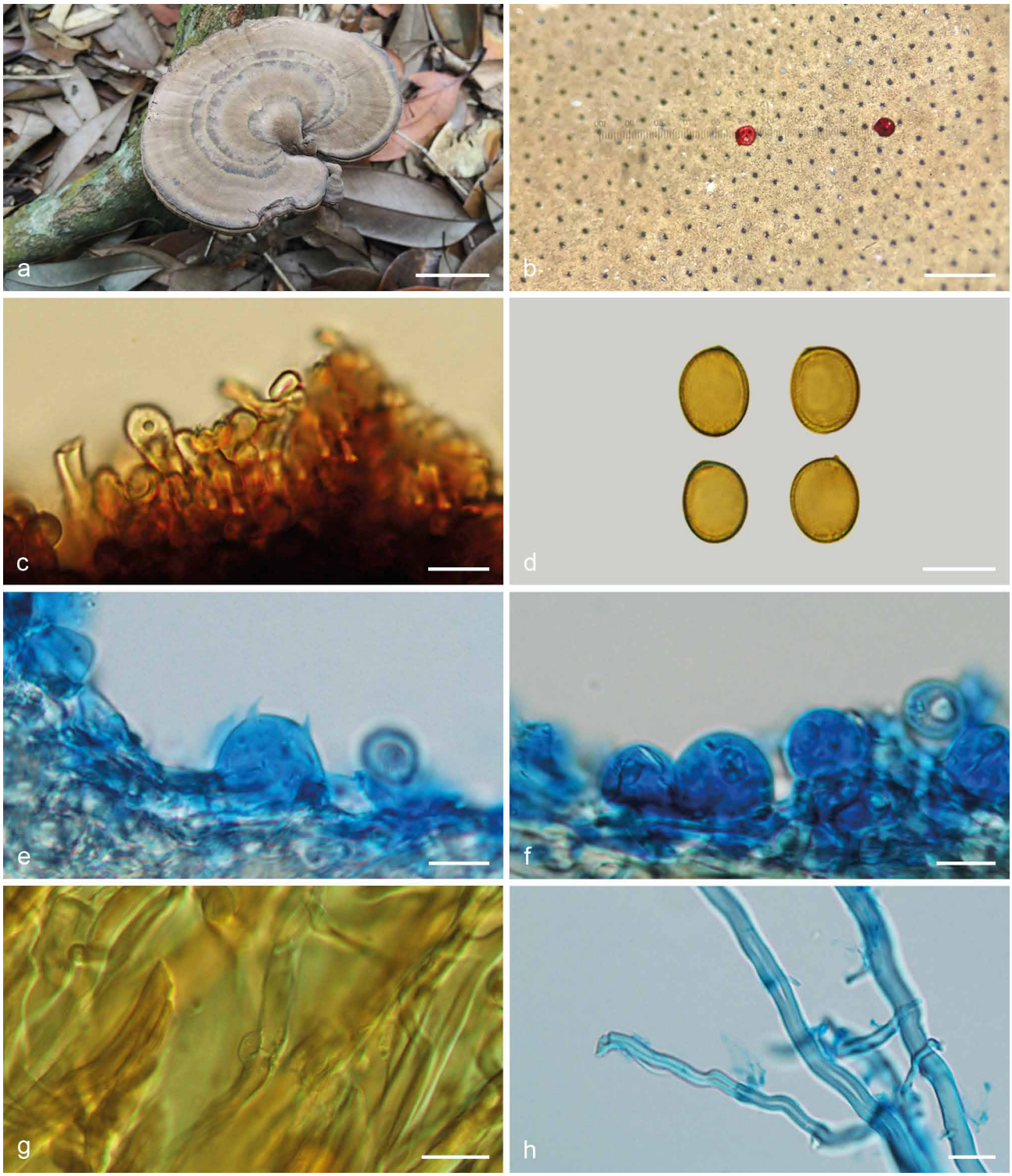

Fig. 13 Basidiomata and microscopic structures of *Sanguinoderma microporum* (Cui 13851). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. generative hyphae from tubes; h. skeletal hyphae from context. — Scale bars: a = 3 cm; b = 0.5 mm; c–h = 10 µm.

less, slightly thick-walled, 3–4 µm diam; skeletal hyphae in tubes pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in tubes pale yellow, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, inflated and flexuous, pale yellow to yellowish brown, about 25–40 × 6–13 µm, forming a regular palisade. *Cystidia* or *cystidioles* absent. *Hymenium* collapsed in the studied sample, basidia and basidioles not seen. *Basidiospores* subglobose to broadly ellipsoid, pale yellow, IKI–, CB+, with double and slightly thick walls, exospore wall smooth, endospore wall with spinules, (10.2–)10.5–12.3(–12.5) × (8.6–)9–10.5(–11.1) µm, L = 11.38 µm, W = 9.71 µm, Q = 1.17 (n = 60/1). Under SEM, exospore wall semi-reticulate, badly worn, endospore wall with long and slightly thick coniform spinules tightly arranged.

Notes — *Sanguinoderma laceratum* can be distinguished by the superposed pileus with slight concentric zones and lacerate pores with thin dissepiments. *Sanguinoderma laceratum* shares a deeply worn exospore wall with *S. bataanense*, but the latter has globose to subglobose basidiospores with distinctly thick walls with a verrucose exospore wall (Fig. 8a–b). In the phylogenetic analyses, *S. laceratum* was shown to be a distinct lineage in *Sanguinoderma* (Fig. 1, 2).

Sanguinoderma microporum Y.F. Sun & B.K. Cui, *sp. nov.* — MycoBank MB828437; Fig. 8i–j, 13

Etymology. *Microporum* (Lat.), refers to the small pores.

Holotype. China, Hainan Province, Qiongzhong County, Limushan National Forest Park, on ground of angiosperm forest, 16 June 2016, *B.K. Cui*, Cui 13851 (BJFC).

Diagnosis. *Sanguinoderma microporum* differs from other species in this genus by its woody hard basidiomata with concentrically zonate or furrowed pileus surface, and small pores with extremely thick dissepiments.

Basidiomata annual, centrally to laterally stipitate, woody hard. Pileus single, suborbicular to flabelliform, up to 10.5 cm diam and 8 mm thick. Pileal surface pale yellowish brown to greyish brown, dull, glabrous, with concentric dark zones or furrows and radial wrinkles; margin acute to obtuse, entire, wavy and incurved when dry. Pore surface yellowish brown to dark brown when fresh, colour changing to blood red when bruised and becoming greyish brown when dry; pores circular, 6–7 per mm; dissepiments extremely thick (about 0.12–0.16 mm thick), entire. Context straw colour, with dark melanoid lines, corky, up to 4 mm thick. Tubes pale brown, up to 4 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, up to 10.5 cm long and 9 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 3–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–8 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, up to 2 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–3 µm diam; skeletal hyphae in tubes pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in tubes colourless, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, faintly inflated and flexuous, pale yellow to dark brown, about 25–40 × 6–13 µm, forming an irregular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 18–22 × 13–18 µm; basidioles in shape similar to basidia, colourless, thin-walled, 16–20 × 10–15 µm. *Basidiospores* broadly ellipsoid, pale yellow, IKI–, CB+, with double and slightly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (10.7–)11–12(–12.3) × (8.5–)8.7–9.8(–10) µm, L = 11.52 µm, W = 9.18 µm, Q = 1.23–1.28 (n = 60/2). Under SEM, exospore wall semi-reticulate, endospore wall with long and slightly thin coniform spinules tightly arranged.

Additional specimens (paratypes) examined. China, Guangdong Province, Zhaoqing, Dinghushan Nature Reserve, on ground of angiosperm forest, 29 June 2010, *B.K. Cui*, Cui 8898 (BJFC); Guangxi Autonomous Region, Fangchenggang, Shiwandashan Nature Reserve, on ground of angiosperm forest, 6 July 2016, *J.L. Zhou*, Cui 14001 (BJFC); ibid., Cui 14022 (BJFC); Nanning, Qingxiushan Park, on ground of angiosperm forest, 3 Aug. 2017, *J.L. Zhou*, Cui 16335 (BJFC); ibid., Cui 16336 (BJFC); ibid., Cui 16338 (BJFC).

Notes — *Sanguinoderma microporum* is a distinct species on account of its distinctly small pores with extremely thick dissepiments. It has broadly ellipsoid basidiospores with slightly thick walls which are similar to *S. laceratum*. But *S. laceratum* differs from *S. microporum* by its superposed pileus and lacerate pores with thin dissepiments. In the phylogenetic analyses, *S. microporum* was shown to be a distinct well-supported lineage in *Sanguinoderma* (Fig. 1, 2).

Sanguinoderma perplexum (Corner) Y.F. Sun & B.K. Cui, *comb. nov.* — MycoBank MB828445; Fig. 8k–l, 14

Basionym. *Amauroderma perplexum* Corner, Beih. Nova Hedwigia 75: 82. 1983.

Basidiomata annual, almost sessile or with a very short and thick stipe, hard corky to woody hard. Pileus single, suborbicular to flabelliform, applanate, up to 11.5 cm long, 8 cm wide and 3 cm thick. Pileal surface reddish brown to ferruginous, dull, glabrous, with concentric furrows and radial wrinkles; margin obtuse, entire, slightly wavy when dry. Pore surface pale white to cream when fresh, colour changing to blood red when bruised, then quickly darkening; pores circular to angular, 5–6 per mm; dissepiments medially thick, entire. Context yellowish brown to cinnamon, with a bunch of melanoid lines, corky, up to 2.4 cm thick. Tubes concolorous with pore surface, hard corky, up to 6 mm long. Stipe concolorous with pileal surface, lateral-attached, up to 2 cm long and 3 cm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 3–5 µm diam; skeletal hyphae in context pale yellow to pale brown, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–7 µm diam; binding hyphae in context colourless, subsolid, branched and flexuous, 1–3 µm diam. Generative hyphae in tubes colourless, thin-walled, 2–4 µm diam; skeletal hyphae in tubes pale yellow to yellowish brown, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in tubes colourless, subsolid, branched and flexuous, 1–3 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells gelatinized, flexuous, yellowish brown, about 30–50 × 4–8 µm, forming an irregular palisade. *Cystidia* absent; cystidioles clavate, colourless, thin-walled, 27–30 × 2–3 µm. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 30–44 × 22–28 µm; basidioles in shape similar to basidia, colourless, thin-walled, 19–30 × 5–11 µm. *Basidiospores* subglobose to broadly ellipsoid, pale yellow, IKI–, CB+, with double and medially thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (11.1–)11.5–14(–14.8) × (9–)10–12(–13.9) µm, L = 12.75 µm, W = 10.84 µm, Q = 1.16–1.19 (n = 60/2). Under SEM, exospore wall densely vermiculate to semi-reticulate, endospore wall with long and thick columnar spinules loosely arranged.

Specimens examined. China, Hainan Province, Changjiang County, Bawangling Nature Reserve, on stump of *Acmena acuminatissima*, 9 May

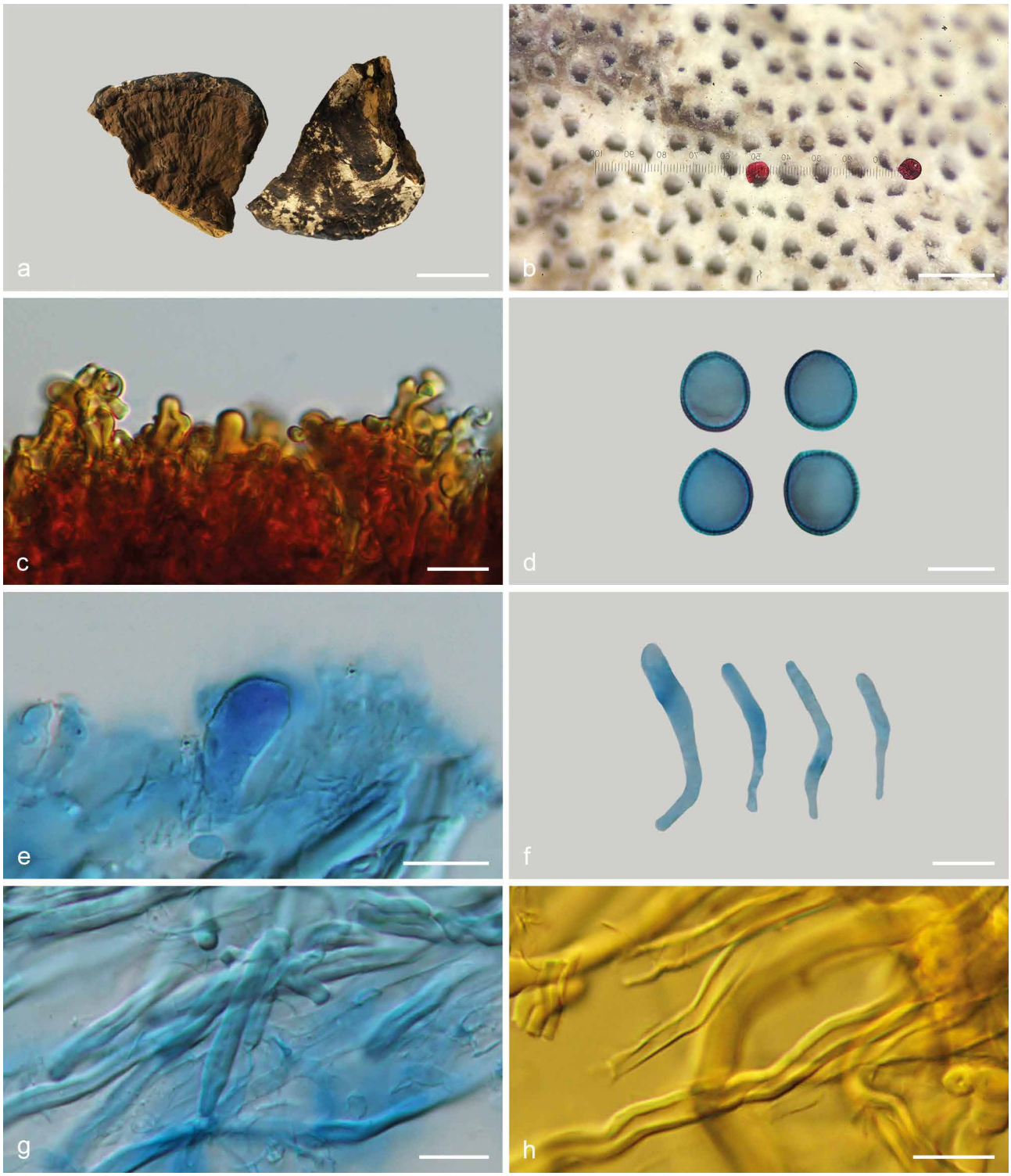

Fig. 14 Basidiomata and microscopic structures of *Sanguinoderma perplexum* (Dai 10811). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidioles; f. cystidioles; g. generative and skeletal hyphae from tubes; h. skeletal hyphae from context. — Scale bars: a = 3 cm; b = 0.5 mm; c–h = 10 µm.

2009, *B.K. Cui*, Cui 6496 (BJFC); on angiosperm stump, 9 May 2009, *Y.C. Dai*, Dai 10811 (BJFC); ibid., 10 May 2009, *B.K. Cui*, Cui 6554 (BJFC).

Notes — *Amauroderma perplexum* was described from Malaysia (Corner 1983). It can be mainly characterized by sessile to substipitate and woody hard basidiomata, clavate cystidioles and a vermiculate to semi-reticulate exospore wall with thick columnar endospore spinules (Fig. 8k–l). In addition, *A. perplexum* presents a pore surface that changes to blood red when bruised and is shown to be a distinct lineage in *Sanguinoderma* with high phylogenetic support (100 % ML, 1.00 BPP). Therefore, we transferred *A. perplexum* to *Sanguinoderma*. *Sanguinoderma perplexum* is similar to *S. laceratum* by sharing broadly ellipsoid basidiospores with slightly thick walls, but *S. laceratum* differs from *S. perplexum* by its thin and lacerate dissepiments and semi-reticulate exospore wall with slightly thin and coniform endospore spinules (Fig. 8g–h).

Sanguinoderma reniforme Y.F. Sun & B.K. Cui, *sp. nov.* — MycoBank MB828438; Fig. 8m–n, 15

Etymology. *Reniforme* (Lat.), refers to the reniform basidiospores.

Holotype. Zambia, Ndola, Ngosa Village, on ground of angiosperm forest, 6 Jan. 2018, *B. Zhang*, Cui 16511 (BJFC; isotype IFP).

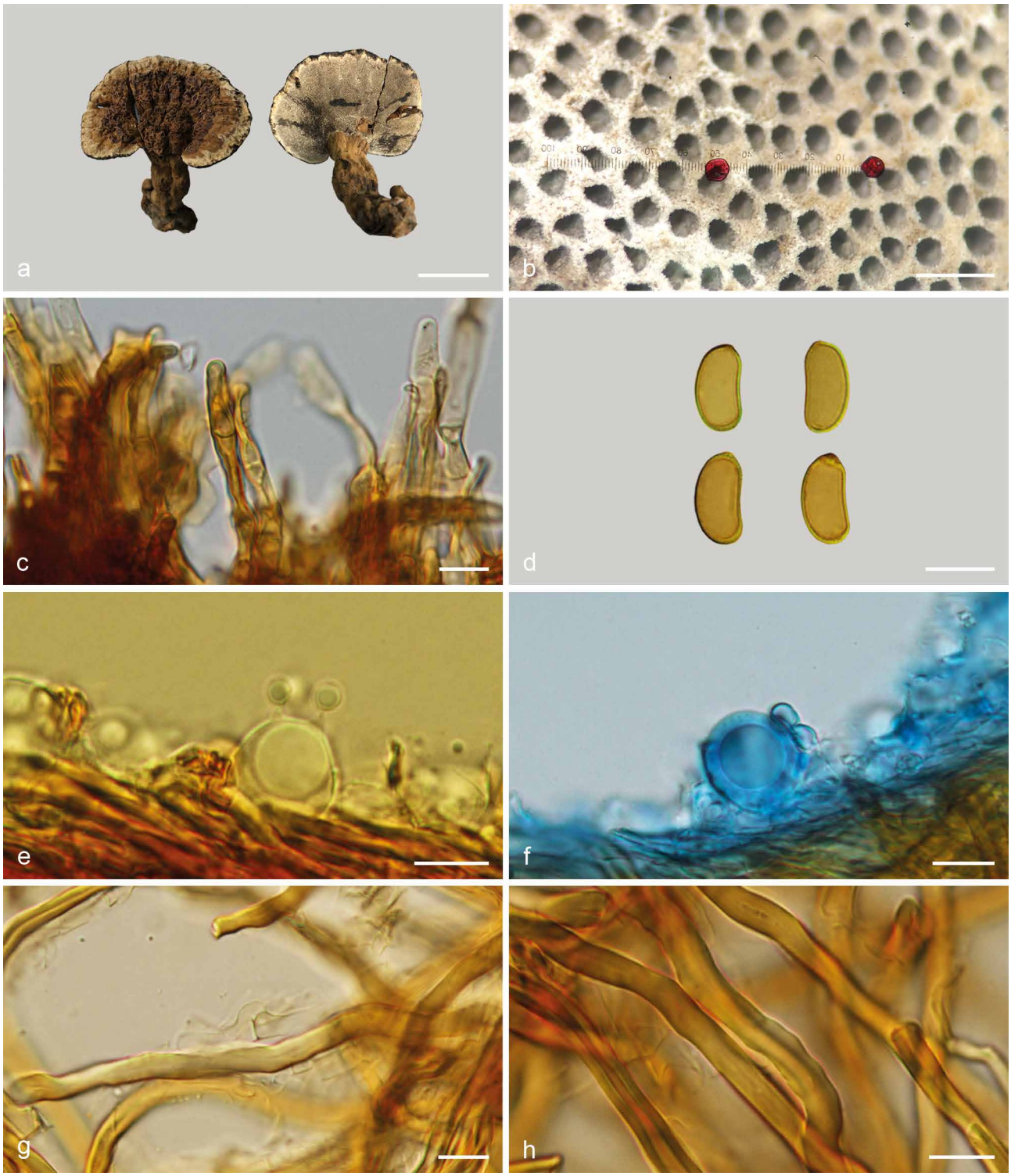

Fig. 15 Basidiomata and microscopic structures of *Sanguinoderma reniforme* (Cui 16511). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. generative hyphae from tubes; h. skeletal hyphae from context. — Scale bars: a = 1.5 cm; b = 0.5 mm; c–h = 10 µm.

Diagnosis. *Sanguinoderma reniforme* differs from other species by its tomentose pileal surface with tumid wrinkles, and reniform basidiospores.

Basidiomata annual, laterally stipitate, hard corky. Pileus single, flabelliform to reniform, up to 4 cm diam and 5 mm thick. Pileal surface yellowish brown to dark yellowish brown, pale yellow in the edge, dull, tomentose, with concentric zones and irregular tumid wrinkles; margin obtuse, entire, slightly wavy and flat when dry. Pore surface pale grey when fresh, colour changing to blood red when bruised, then quickly darkening; pores circular to angular, 4–5 per mm; dissepiments slightly thick, entire. Context pale yellowish brown, with variegated resinous stratum, hard corky, up to 3 mm thick. Tubes concolorous with pore surface, corky, up to 2 mm long. Stipe concolorous with pileal surface, cylindrical, swollen at the base, up to 5 cm long and 1 cm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 3–5 µm diam; skeletal hyphae in context pale yellow to yellowish brown, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–7 µm diam; binding hyphae in context pale yellow, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, thin-walled, 3–4 µm diam; skeletal hyphae in tubes pale yellow to yellowish brown, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in tubes pale yellow, subsolid, branched and

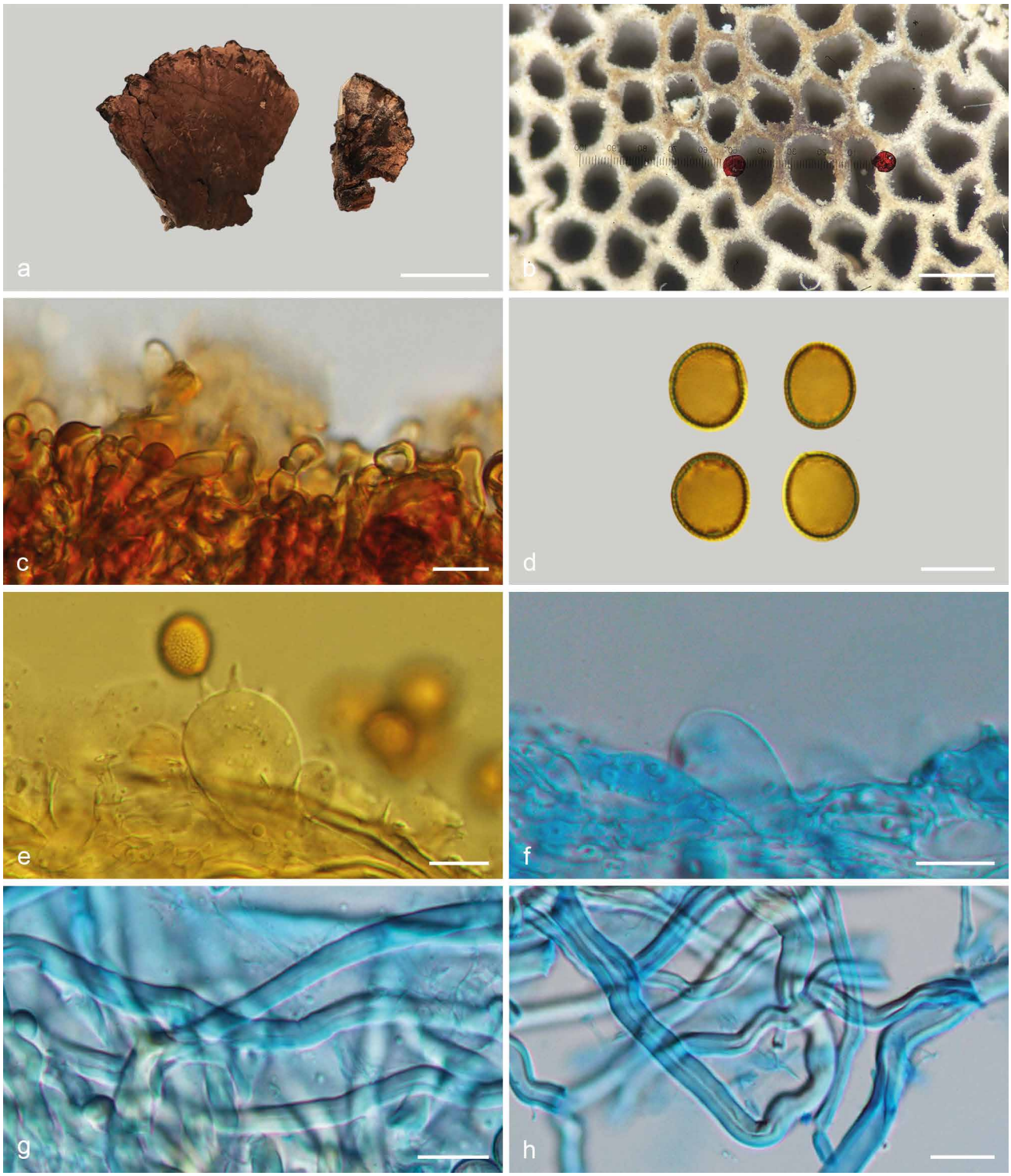

Fig. 16 Basidiomata and microscopic structures of *Sanguinoderma rude* (MEL 2335651). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. skeletal hyphae from tubes; h. skeletal hyphae from context. — Scale bars: a = 3 cm; b = 0.5 mm; c–h = 10 µm.

flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, constricted, flexuous, pale yellowish brown, about 40–70 × 5–7 µm, forming an irregular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 18–23 × 14–16 µm; basidioles in shape similar to basidia, colourless, thin-walled, 18–20 × 7–15 µm. *Basidiospores* reniform, pale yellow, IKI–, CB+, with double and slightly thick walls, exospore wall smooth, endospore wall with faint spinules, (11–)11.2–13 (–13.3) × (5.5–)5.7–7(–7.3) µm, L = 12.12 µm, W = 6.35 µm, Q = 1.91 (n = 60/1). Under SEM, exospore wall obviously verrucose or semi-reticulate, endospore wall with short and slightly thick coniform spinules tightly arranged.

Notes — *Sanguinoderma reniforme* was collected from Zambia and it is unique in the genus due to its reniform basidiospores. In addition, *S. reniforme* was shown to be a distinct lineage in *Sanguinoderma* (Fig. 1, 2).

Sanguinoderma rude (Berk.) Y.F. Sun, D.H. Costa & B.K. Cui, *comb. nov.* — MycoBank MB828446; Fig. 8o–p, 16

Basionym. Polyporus rudis Berk., Ann. Mag. Nat. Hist. 3: 323. 1839.
≡ *Amauroderma rude* (Berk.) Torrend, Brotéria, Sér. Bot. 18: 127. 1920.

Basidiomata annual, lateral stipitate to almost sessile, corky. Pileus single, suborbicular to flabelliform, up to 7.5 cm diam and 1.7 cm thick. Pileal surface dark brown to ferruginous, dull,

glabrous, with faintly concentric zones and radial wrinkles; margin acute to obtuse, entire, wavy and incurved when dry. Pore surface pale grey to greyish yellow, colour changing to blood red when bruised, then quickly darkening; pores subcircular to irregular, 1–4 per mm; dissepiments slightly thick, entire. Context woody colour to pale brown, without resinous lines, soft corky, up to 9 mm thick. Tubes darker than pore surface, hard corky, up to 8 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, up to 5 cm long and 4 mm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin- to slightly thick-walled, 2–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 2–8 µm diam; binding hyphae in context pale yellow, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, thin- to slightly thick-walled, 2–4 µm diam; skeletal hyphae in tubes pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae in tubes pale yellow, subsolid, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, faintly inflated, flexuous, yellowish brown, about 40–80 × 4–6 µm, forming an irregular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 13–33 × 12–28 µm; basidioles suborbicular to clavate, colourless,

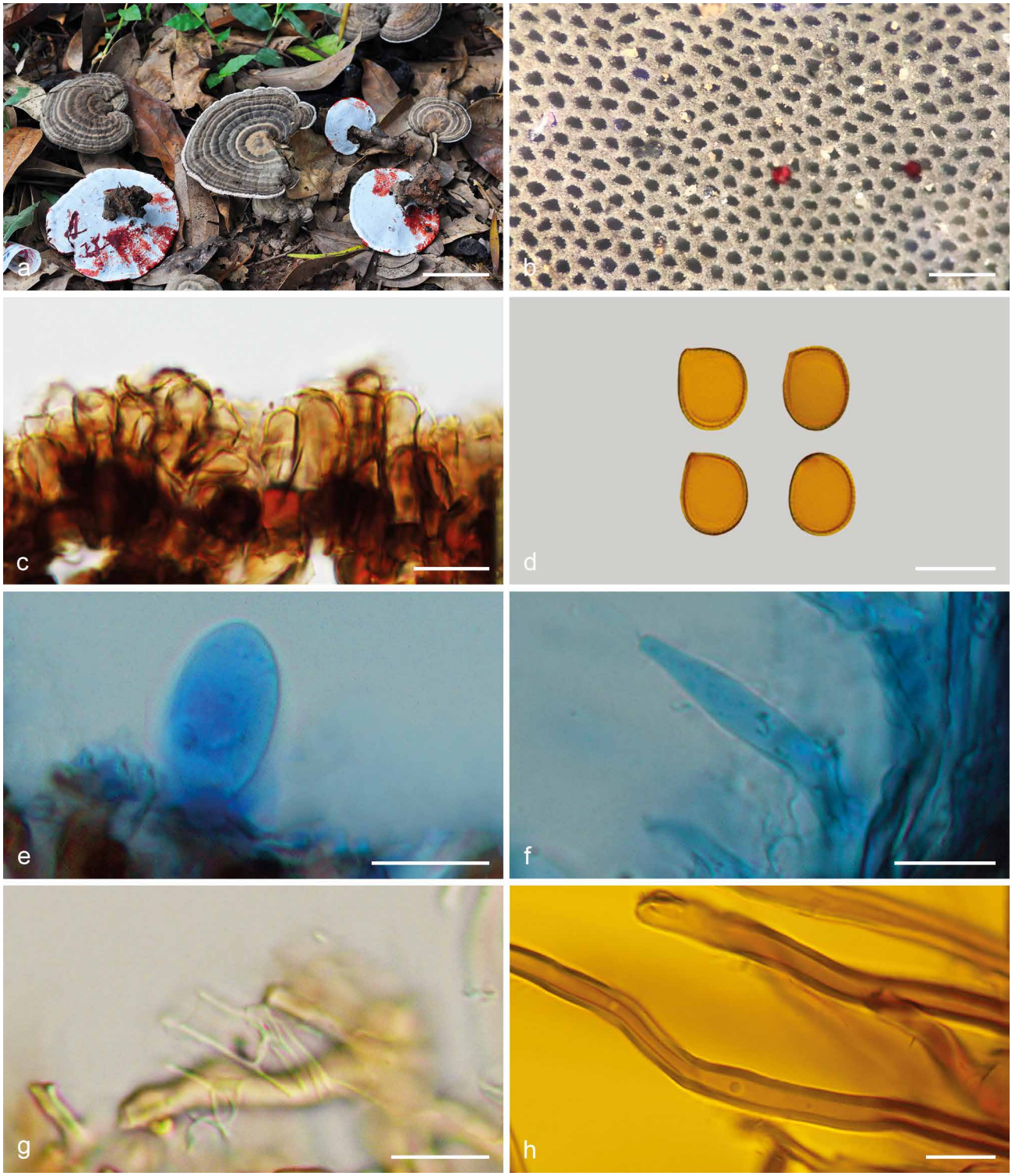

Fig. 17 Basidiomata and microscopic structures of *Sanguinoderma rugosum* (Cui 16337). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidioles; f. cystidioles; g. generative hyphae from tubes; h. skeletal hyphae from context. — Scale bars: a = 4 cm; b = 0.5 mm; c–h = 10 µm.

thin-walled, 15–25 × 8–19 µm. *Basidiospores* subglobose to broadly ellipsoid, pale yellow, IKI–, CB+, with double and medially thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (9–)9.5–12.5(–12.9) × 8–10.7(–11) µm, L = 11.18 µm, W = 9.5 µm, Q = 1.17–1.19 (n = 60/2). Under SEM, exospore wall alveolate to semi-reticulate with small and deep pits, endospore wall with short and slightly thick columnar spinules tightly arranged.

Specimens examined. Australia, Victoria State, Eastern Highlands, on rotten stump, 20 Mar. 1994, *N.H. Sinnott*, MEL 2028873 (MEL); East Gippsland, on buried wood, 27 Mar. 2002, *K.R. Thiele*, MEL 2150776 (MEL); Eastern Highlands, on stump of *Eucalyptus*, 12 May 2003, *S.H. Lewis*, MEL 2231602 (MEL); Gippsland Plain, on rotten stump of shrub, 4 May 2007, *H. Strand*, MEL 2317411 (MEL); Fairfield, on rotten stump of *Acacia*, 23 Apr. 2009, *N.H. Sinnott*, MEL 2335651 (MEL); Valley Reserve, on rotten wood, 14 July 2012, *N.G. Karunajeewa*, MEL 2362204 (MEL); Tasmania, on base of dead *Eucalyptus*, 12 May 2018, *B.K. Cui*, Cui 16592 (BJFC).

Notes — *Amauroderma rude* was described from Tasmania as *Polyporus rudis* (Berkeley 1839). We have examined the specimens collected from the type locality of Tasmania and mainland in Australia. It can be characterized by its big pores (1–4 per mm) with slightly thick and entire dissepiments, and alveolate to semi-reticulate exospore wall with small and deep pits (Fig. 8o–p). *Amauroderma rude* was shown as a distinct well-supported lineage in *Sanguinoderma* (Fig. 1, 2). *Sanguinoderma rude* is similar to *S. perplexum* by the subglobose to broadly ellipsoid basidiospores, but *S. perplexum* differs from *S. rude* by the woody hard basidiomata, small pores (5–6 per mm) with medially thick dissepiments and vermiculate to semi-reticulate exospore wall with long and thick endospore spinules (Fig. 8k–l). *Amauroderma intermedium* is quite similar to *S. rude* both in macro- and micro-morphology (Gomes-Silva et al. 2015), but it can be distinguished by its Neotropical distribution, darker context and colour-unchanging pore surface when bruised (Torrend 1920, Ryvarden 2004).

Sanguinoderma rugosum (Blume & T. Nees) Y.F. Sun, D.H. Costa & B.K. Cui, *comb. nov*. — MycoBank MB828447; Fig. 8q–r, 17

Basionym. *Polyporus rugosus* Blume & T. Nees, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 13: 21. 1826.

≡ *Amauroderma rugosum* (Blume & T. Nees) Torrend, Brotéria, Sér. Bot. 18: 127. 1920.

Basidiomata annual, centrally to laterally stipitate, corky to woody hard. Pileus single, suborbicular to flabelliform, up to 12 cm diam and 8 mm thick. Pileal surface dark brown to near black, dull, glabrous, with obviously concentric furrows and radial wrinkles, centre navel-shaped; margin acute to obtuse, entire, wavy and incurved when dry. Pore surface greyish white when fresh, colour changing to blood red when bruised, then quickly darkening; pores circular to angular, 5–7 per mm; dissepiments slightly thick, entire. Context cinnamon to dark brown, with two black resinous lines, corky, up to 5 mm thick. Tubes concolorous with pore surface, woody hard, up to 3 mm long. Stipe concolorous with pileal surface, cylindrical and hollow, slightly swollen at base, up to 12 cm long and 1 cm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 4–6 µm diam; skeletal hyphae in context yellowish brown to dark brown, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 4–6 µm diam; binding hyphae in context pale yellow, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes scanty; skeletal hyphae in tubes dark brown, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–7 µm diam; binding hyphae in tubes pale brown, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate with obvious septa at the base, inflated, dark brown, about 20–50 × 6–10 µm, forming a regular palisade. *Cystidia* absent; cystidioles clavate and apexes constricted, colourless, thin-walled, 20–28 × 3–5 µm. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 18–25 × 9–20 µm; basidioles in shape similar to basidia, colourless, thin-walled, 15–20 × 10–16 µm. *Basidiospores* broadly ellipsoid, pale yellow, IKI–, CB+, with double and slightly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (9.9–)10.2–11.3(–11.7) × (8–)8.3–9.2(–9.5) µm, L = 10.75 µm, W = 8.86 µm, Q = 1.21–1.22 (n = 60/2). Under SEM, exospore wall alveolate to semi-reticulate, endospore wall with short and thin columnar spinules tightly arranged.

Specimens examined. China, Guangdong Province, Shaoguan, Chebaling Nature Reserve, on ground of angiosperm forest, 25 June 2010, *B.K. Cui*, Cui 8795 (BJFC); Zhaoqing, Heishiding Nature Reserve, on ground, 1 July 2010, *B.K. Cui*, Cui 9011 (BJFC); ibid., Cui 9012 (BJFC); Guangxi Autonomous Region, Nanning, Liangfengjiang National Forest Park, on ground, 3 Aug. 2017, *J.L. Zhou*, Cui 16337 (BJFC); ibid., 4 Aug. 2017, Cui 16166 (BJFC). – Indonesia, West Java, Banten, on *Acacia mangium*, *Bougher*, E7079 (PERTH).

Notes — *Amauroderma rugosum* is a widespread species distributed in tropical and subtropical areas of South East Asia. It seems to be a species of difficult delimitation due to its great spectrum of morphologic variation (colour, texture and basidiospores size), exhibiting a broadly distribution (although some of the records are dubious), being one of the most cited *Amauroderma* species (Furtado 1981, Corner 1983). Based on its colour-changing pore surface when bruised and good phylogenetic support, it is proposed as a new combination in *Sanguinoderma*. It is similar to *S. microporum* in the dark brown pileal surface with obvious concentric furrows and radial wrinkles, but *S. microporum* differs from *S. rugosum* by the extremely thick dissepiments and slightly bigger basidiospores (11–12 × 8.7–9.8 µm) with long and thin endospore coniform spinules (Fig. 8i–j). The distinction between *S. rugosum* and *S. rude* is difficult, but the latter has a softer pileus and slightly larger spores (9.5–12.5 × 8–10.7 µm).

Sanguinoderma sinuosum Y.F. Sun & B.K. Cui, *sp. nov*. — MycoBank MB828439; Fig. 8s–t, 18

Etymology. *Sinuosum* (Lat.), refers to the sinuate pores.

Holotype. Australia, Queensland State, Sunshine Coast, on sandy ground, 7 Mar. 2010, *P. Leonard*, MEL 2366586 (MEL).

Diagnosis. *Sanguinoderma sinuosum* differs from other species in this genus by its sinuate pores with thin dissepiments, big and broadly ellipsoid to ellipsoid basidiospores.

Basidiomata annual, centrally to laterally stipitate, soft to hard corky. Pileus single, suborbicular to flabelliform, up to 6.5 cm diam and 1.6 cm thick. Pileal surface dark brown to ferruginous when dry, dull, glabrous, with obvious concentric furrows and strong radial wrinkles; margin obtuse, entire, wavy and incurved when dry. Pore surface pale white when fresh, colour changing to blood red when bruised, then quickly darkening; pores sinuate, 2–3 per mm; dissepiments thin, entire. Context straw colour to cinnamon, with pale white lines, soft corky, up to 7 mm thick. Tubes cinnamon, woody hard, up to 9 mm long. Stipe concolorous with pileal surface, cylindrical and flexuous, up to 6 cm long and 1.5 cm diam. *Hyphal system* trimitic; generative hyphae with clamp connections, all hyphae IKI–, CB+; tissues darkening in KOH. Generative hyphae in context colourless, thin-walled, 2–4 µm diam; skeletal hyphae in context pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, 3–6 µm diam; binding hyphae colourless to pale yellow, subsolid, branched and flexuous, 1–2 µm diam. Generative hyphae in tubes colourless, up to

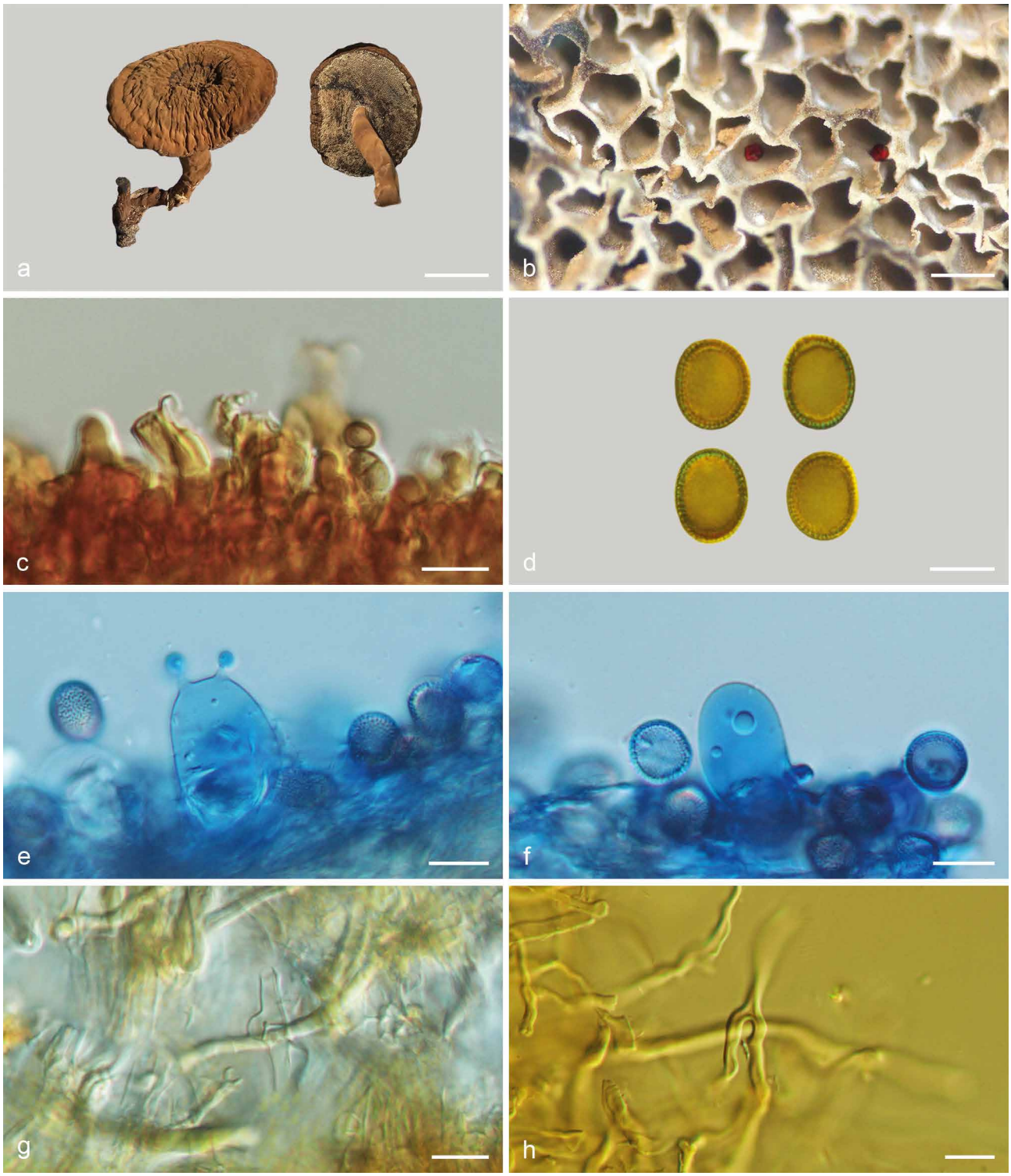

Fig. 18 Basidiomata and microscopic structures of *Sanguinoderma sinuosum* (MEL 2366586). a. Basidiomata; b. pores; c. apical cells from pileal cover; d. basidiospores; e. basidia; f. basidioles; g. generative hyphae from tubes; h. skeletal hyphae from context. — Scale bars: a = 2.5 cm; b = 0.5 mm; c–h = 10 µm.

3 µm diam; skeletal hyphae in tubes colourless to pale yellow, thick-walled with a wide to narrow lumen or subsolid, arboriform branched and flexuous, up to 5 µm diam; binding hyphae in tubes pale yellow, subsolid, branched and flexuous, 1–2 µm diam. *Pileal cover* composed of clamped generative hyphae, thin- to thick-walled, apical cells clavate, faintly inflated, pale yellowish brown, about 50–70 × 4–6 µm, forming an irregular palisade. *Cystidia* or *cystidioles* absent. *Basidia* barrel-shaped to clavate, colourless, thin-walled, 25–33 × 15–19 µm; basidioles in shape similar to basidia, colourless, thin-walled, 23–28 × 13–16 µm. *Basidiospores* broadly ellipsoid to ellipsoid, pale yellow to yellowish brown, IKI–, CB+, with double and slightly thick walls, exospore wall smooth, endospore wall with conspicuous spinules, (12.3–)12.5–13.7(–14.3) × 9.1–10.8(–11.1) µm, L = 13.07 µm, W = 10.08 µm, Q = 1.3 (n = 60/1). Under SEM, exospore wall uneven, with distinctly circular hollows, endospore wall with long and thick columnar spinules tightly arranged.

Additional specimen (paratype) examined. Australia, Victoria State, Langwarrin Flora and Fauna Reserve, on rotten stump of *Acacia*, 6 June 2010, *N.H. Sinnott*, MEL 2341763 (MEL).

Notes — *Sanguinoderma sinuosum* was collected from Australia. It is characterized by its sinuate pores with thin dissepiments, large and broadly ellipsoid to ellipsoid basidiospores. *Sanguinoderma sinuosum* is similar to *S. rude* by the dark

Table 2 The distribution and main morphological differences of accepted genera in *Amauroderma* s.lat.

Genus	Distribution	Pileal surface	Pore surface	Hyphal system	Shape of basidiospores	Ornamentation of basidiospores	References
Amauroderma s.str.	most neotropical areas	brown to near black, dull to laccate, glabrous to tomentose	pale white to yellowish brown, colour unchanged when bruised	dimitic	globose or ellipsoid to obovoid	endospore wall smooth or ornamented	Gomes-Silva et al. 2015, Costa-Rezende et al. 2016
Foraminispora	South China, Central and South America	yellowish brown to reddish brown, dull, tomentose	white to straw colour, colour unchanged when bruised	dimitic to trimitic	globose to ellipsoid	exospore wall uneven or foveolate, endospore wall with hollow and columnar spinules which persist to exospore wall forming holes	Costa-Rezende et al. 2017, present study
Furtadoa	Central and South America	yellowish brown to greyish brown, dull, glabrous to tomentose	white to straw colour, colour unchanged when bruised	monomitic to dimitic	subglobose to ellipsoid	endospore wall with conspicuous spinules	Gomes-Silva et al. 2015, Costa-Rezende et al. 2017
Sanguinoderma	Asia, South Africa and Oceania	dark brown to near black, dull, glabrous to tomentose	grey white to dark grey, colour changed to blood red when bruised	trimitic	subglobose or ellipsoid to reniform	exospore wall semi-reticulate or vermiculate to verrucose, endospore wall with solid and columnar to coniform spinules	present study

brown and corky pileus with concentric furrows and radial wrinkles, but *S. rude* has subcircular pores with slightly thick dissepiments, and smaller basidiospores (9.5–12.5 × 8–10.7 µm) with short and slightly thick columnar endospore spinules (Fig. 8o–p). In the phylogenetic analyses, these two species nested in two lineages with good support (Fig. 1, 2).

DISCUSSION

Costa-Rezende et al. (2017) provided a phylogenetic analysis on *Amauroderma* s.lat. based on 4-gene sequences (ITS+nLSU+*TEF*+*RPB1*) with main focus on samples from Neotropics and indicated that *Amauroderma* was polyphyletic. In the current study, taxonomic and phylogenetic analyses of *Amauroderma* s.lat. were carried out based on samples from Africa, Asia and Oceania and more gene markers (ITS+nLSU+*TEF*+*RPB1*+*RPB2*+*TUB*). Our results also confirmed the polyphyly of *Amauroderma* and that species previously belonging to *Amauroderma* s.lat. are divided into four clades representing four genera: *Amauroderma* s.str., *Foraminispora* and *Furtadoa*, as already shown by Costa-Rezende et al. (2017), and the new genus *Sanguinoderma*. This division was also supported by morphology and ultrastructural features, and the classification system of *Amauroderma* s.lat. was revised. The distribution and main morphological differences of accepted genera in *Amauroderma* s.lat. are shown in Table 2. Besides the new genus, six new species and eight new combinations have been proposed and described.

The examination of fresh specimens previously classified in *Amauroderma* and some undescribed taxa showed the presence of a striking reaction on pore surface, which changes almost instantaneously to blood red when bruised, and then turns to a dark coloration. This reaction was already reported by Corner (1983) for *A. atrum*, *A. perplexum* and *A. rugosum*. The phylogenetic results showed that all the sampled species which present this reaction grouped together. Then, we proposed the genus *Sanguinoderma* to accommodate those species. Some macro-fungi present the amino acid tyrosine, which is enzymatically oxidized to a red intermediate and further to melanin and acts as a bioactive agent against microbes and harming substances (Halbwachs et al. 2016), which could be the case of *Sanguinoderma* species.

The new genus comprises the species from tropical Asia, Africa and Oceania. *Sanguinoderma* and *Amauroderma* s.str. share stipitate to almost sessile and corky to woody hard basidiomata, glabrous to tomentose and concentrically zonate or furrowed pileal surface and double-walled basidiospores. However, *Sanguinoderma* may be distinguished from *Amauroderma* s.str. by the fresh pore surface colour that changes to blood red when bruised. In addition, *Amauroderma* s.str. has a neotropical distribution (Gomes-Silva et al. 2015, Costa-Rezende et al. 2016, 2017, Song et al. 2016), while *Sanguinoderma* is distributed in the Paleotropical region and Oceania.

The species in *Amauroderma* s.str. have a dull to laccate pileal surface, a fresh pore surface colour unchanging when bruised, a dimitic hyphal system and non-dextrinoid or dextrinoid basidiospores with solid endospore ornamentation (Ryvarden 2004, Gomes-Silva et al. 2015, Song et al. 2016, Costa-Rezende et al. 2017). Up to now, *Foraminispora* was considered as a monotypic genus, composed only by *F. rugosa* from Neotropics (Costa-Rezende et al. 2017). During the study of basidiospores ultrastructure of tropical and subtropical species previously classified in *Amauroderma* (*A. austrosinense*, *A. concentricum* and *A. yunnanense*) and one undescribed species, we observed that those species presented basidiospores with the typical morphology of *Foraminispora*. Besides that, those species grouped together with *F. rugosa* in our phylogenetic study.

Thus, we propose here three new combinations and one new species for *Foraminispora*. All these five species are similar to *Amauroderma* s.str. species by stipitate and corky to woody hard basidiomata, fresh pore surface colour unchanging when bruised, similar hyphal system and non-truncate, double-walled, indextrinoid or dextrinoid basidiospores. But *Foraminispora* is unique on account of the globose to ellipsoid basidiospores with hollow and columnar endospore spinules, which persist to the exospore wall forming holes sometimes which can be viewed under SEM (Fig. 3). So far, *Foraminispora* is composed of five species, of which four are found in temperate or subtropical regions of East Asia and one in neotropical areas.

Furtadoa comprises two species from Neotropics, which have stipitate and fleshy basidiomata with a dull pileal surface, a fresh pore surface colour unchanging when bruised, and a monomitic context with both clamped and simple septate generative hyphae (Gomes-Silva et al. 2015, Costa-Rezende et al. 2017). Based on these features, *Furtadoa* can be easily distinguished from the other three genera.

Scanning electron microscopy (SEM) had been widely used in the taxonomy of *Basidiomycota*, such as *Russulales* (Lebel & Trappe 2000), *Bondarzewia* (Chen et al. 2016) and *Phylloporus* (Zeng et al. 2013). Costa-Rezende et al. (2017) established *Foraminisprora* based on its unique ultrastructural characters of the basidiospores, as mentioned above. In our study and in addition to the molecular analyses, the basidiospores of *Foraminispora* and *Sanguinoderma* were also scanned by SEM and we observed the ornamentations on the endospore and exospore walls of *Sanguinoderma* are quite different from those of *Foraminispora*. Spores of *Sanguinoderma* have a semi-reticulate or vermiculate to verrucose exospore wall and an endospore wall with solid and columnar to coniform spinules (Fig. 8). According to our observations and previous descriptions, we consider that SEM is a far more important taxonomic method in the identification of genera than species within *Ganodermataceae*.

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